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GEOLOGY.—*Our petroleum supply.*[1] HUGH D. MISER, U. S. Geological Survey.

The petroleum supply of the United States is of great importance, whether we express the volume and value of the annual output in barrels or dollars, or measure the service of petroleum in terms of human welfare and progress.

Petroleum is produced in many countries, and its products are used in factories, on highways, and in homes in all lands. Although the petroleum industry thus encircles the earth, it is outstandingly an American industry. The drilling of wells for oil in the United States began in 1859. Our country leads in the development of the industry, and it produces and consumes three-fifths of the world's annual output. Also, the United States possesses about half of the world's known reserves of petroleum.

PRESENT PRODUCTION AND USES OF PETROLEUM IN UNITED STATES

Our domestic petroleum production is obtained from about 360,000 wells in 22 States; only a small part—about 5 per cent—of our domestic consumption is imported from other countries.

The value of our petroleum output for 1937 measured in dollars is one-fourth the value of the entire annual mineral production of the United States. It exceeds the total value of all the metallic mineral products combined for that year. The next mineral product in point of value is coal, the next is iron, and then follows natural gas.

Chief among the many uses of petroleum is the production of power. Such power drives our 30,000,000 motor vehicles on the land, our Navy on the ocean, and our planes in the air. Altogether, one-third the mechanical energy produced in the United States comes from petroleum and its companion mineral product, natural gas.

Our domestic production through 1937 totals 19,972,000,000 barrels. Texas stands first, having produced 5,127,000,000 barrels, a

[1] Address of the retiring president of the Geological Society of Washington, delivered December 14, 1938. Published by permission of the Director, Geological Survey, United States Department of the Interior. Received December 15, 1938.

quarter of all the Nation's output of oil. California has produced 4,872,000,000 barrels, 24 per cent, and Oklahoma 4,341,000,000 barrels, 21 per cent. The output of no other State has equaled the domestic demand of petroleum products for the year 1937—namely, 1,169,000,000 barrels.

Altogether, Texas, California, and Oklahoma have contributed 72 per cent of all the oil output of the United States. The total production of each of these States is greater than that of the U.S.S.R.—3,771,000,000 barrels through 1937—which ranks next to the United States in point of cumulative production. Mexico ranks third in total world output, with 1,863,000,000 barrels, and Venezuela fourth, with 1,491,000,000 barrels. No other oil-producing country has produced as much as one billion barrels.

The principal petroleum products and their uses form long lists whose presentation time does not now permit. A general grouping of the refined products includes gasoline, kerosene, fuel oils, lubricants, paraffin wax, petroleum coke, asphalt, road oil, petrolatum, absorption oil and medicinal oil.

Kerosene, the first petroleum product to be utilized in important quantities, is still extensively used for lighting. In addition, it is utilized in increasing volumes to provide power and heat.

The domestic demand for gasoline in 1937 was 519,000,000 barrels, for use chiefly in our motor vehicles. The automobile depends heavily on the petroleum industry; it consumes 89 per cent of our gasoline, 40 per cent of our lubricants, and requires natural gas derived carbon black which lengthens 2½ to 3 times the lifetime of our tires. The domestic demand for gasoline is directly related to the number of motor vehicles, which average one to about every five persons. The volume of consumed gasoline, since the introduction of the first American automobile in 1892, parallels the increasing numbers of motor cars. In late years the slight departure from parallelism is due to the greater volume of gasoline used by each car and to the increased use of gasoline in airplanes, tractors, motor boats, and stationary engines. Second only to gasoline were the requirements for fuel oil—442,000,000 barrels in 1937—which is used by railroads, steamships, gas and electric power plants, mines, smelters, manufacturing plants, oil companies, and U. S. Navy, and for domestic heating. The development of our machine age has depended on a plentiful supply of lubricants made from petroleum. The great volume of demand—23,323,000 barrels in 1937—can be met only by obtaining it from petroleum.

Our petroleum output, as thus briefly described, is provided by one

of the Nation's most important industries. The investment in the United States in the five divisions—the producing, natural gasoline, transportation, refining, and marketing divisions—of the petroleum industry totals about $14,000,000,000.

EARLY DEVELOPMENT AND USES OF PETROLEUM

Before 1859 petroleum and its associated hydrocarbons had been used by the peoples of many lands for at least several thousand years before the Christian era. Seepages and hand-dug pits and shafts provided the entire supply of these materials, except in India and China where oil was obtained from drilled wells. The Chinese, by sinking wells to depths of 1,500 to 2,000 feet for brine, oil, and gas, were recognized as the ancient world's most accomplished well drillers.

The early uses for petroleum and its products were many, as will be noted below.

Asphaltic pitch was used to waterproof the ark of Noah, the cradle of Moses, and the cisterns and silos of ancient Egypt and Mesopotamia. Also, it was used by the Egyptians in the process of mummification. Asphalt was used as a mortar in the construction of Nineveh and Babylon and also in the buried cities of Ur, as early as 4000 B.C. Oil from Sicily was used by the Romans to light the temple of Jupiter, and many centuries later flame throwers fed by naphtha were employed against the Crusaders when they stormed the walls of Constantinople. Petroleum was distilled into products of commerce at Baku as early as the 18th century; oil was there used in lamps and also was utilized for cooking in 1723. In Rumania the exploitation of oil by shafts dates as far back as the second half of the 16th century. To Rumania is ascribed the first recorded volume of output of crude petroleum. In 1857 that country produced 1,977 barrels and since then it has an unbroken record of production.

The early American Indians were familiar with natural petroleum seepages. They set their mosaics in asphaltum; they used it as an adhesive substance; they lined their baskets with it; and they had great faith in petroleum for performing all manner of cures.

Oil and gas were known and used before 1859 in many other countries. A search and study of the literature concerning their recovery, transportation, treatment, and utilization before that date reveals a fascinating story of the progress of human civilization.

At the beginning of the 19th century, when the supply of whale oil for lighting needs was dwindling, the world was faced with the necessity of finding a reasonably priced substitute for it. This necessity

stimulated the research—already being conducted—in the distillation of oil from coal and shale. Paraffin was extracted from both bituminous shale and crude petroleum in France in 1830. Burning oil in commercial quantity was first produced from shale in France in 1838. The refining of oil at the Riddings Colliery in Derbyshire was begun in 1848 by James Young and he later obtained oil from coal and bituminous shales. He founded in 1851 the Scotch industry for the extraction of oil and paraffin from boghead coal. His process for obtaining illuminating oil was rewarded with commercial success, and during the next 10 years its use expanded rapidly in Great Britain and was introduced into the United States. American coals were treated in plants in Pennsylvania, West Virginia, Kentucky, and Ohio. This rising industry was soon replaced by the petroleum industry.

During the first half of the 19th century increasing quantities of crude petroleum, known as rock oil, were obtained from seepages and from wells drilled for salt brines in Pennsylvania, Ohio, Kentucky, and West Virginia, but very little of it was marketed. Between 1850 and 1855 petroleum from a salt well at Tarentum, Pa., was refined in Pittsburgh and sold for lamp use. Also by 1850 some oil from the locality was bottled and sold by druggists; and about 1855 the oil was refined by methods used for the recovery of oil from coal.

The salt wells in Pennsylvania and the nearby States had been drilled with equipment designed for the purpose. This equipment, which embodied the fundamental features of the modern standard cable drill rig, was developed in 1806–1808 in the Kanawha Valley, West Virginia. Accordingly, salt well drillers and their equipment were employed for the drilling in 1859 of the Drake well near Titusville, Pa., in which it was hoped that there would be obtained a larger supply of oil than that afforded by the oil springs of the locality. The Drake well, on reaching a depth of 69½ feet, discovered oil and its initial daily output was 25 barrels. This was America's first commercial oil well.

RELATION OF GEOLOGY TO PETROLEUM INDUSTRY

The phenomenal growth of the petroleum industry in the United States has been aided greatly by engineering and science. In the words of W. C. Teagle, formerly President of the Standard Oil Co. of New Jersey, "The operation of the world's oil industry is now very largely in the hands of technical experts, geologists, physicists, chemists, and

engineers. This change in the complexion of the responsible operating personnel has occurred more rapidly, perhaps, than in any other field of comparable importance (17)." On the same subject Lord Cadman, head of many British petroleum companies and past president of the Institution of Petroleum Technologists, comments, "In no branch of human endeavor has the application of exact knowledge been so apparent as in the exploring, winning, refining, transport, distribution, and utilization of mineral oil. At every point in the long road that leads from the oil well to the consumer investigation and research have been employed with almost spectacular results (2)."

The recognition of the value of the geologists' contribution to the industry finds concrete expression in the fact that most of the companies have geological departments. Oil companies, however, have employed great numbers of geologists only in the last 25 years.

The general acceptance of geology in the search for oil took place about 1915, more than 50 years after the completion of the Drake well. This acceptance was not so much a whole-hearted welcome as it was a necessity, for the oil companies were being pressed to meet the rapidly increasing demands for gasoline required for the growing numbers of motor vehicles.

Although geology was utilized only to a limited extent in the selection of drilling sites during the first half century of the petroleum industry, geologic observations concerning the occurrence of petroleum date back to 1842. In that year William Logan observed the occurrence of oil on anticlines near Gaspé. In 1860 H. D. Rogers noted that the newly discovered fields in Pennsylvania were located on anticlines. In the following year T. Sterry Hunt outlined the first clear statement of the anticlinal theory of the accumulation of petroleum but during the next 25 years Hunt and the other geologists who accepted the anticlinal theory made little application of it in reporting on the oil possibilities of certain areas in the United States and Canada. In the early eighties I. C. White made practical application of the principles of the theory in the location of new oil and gas fields, but still the industry in general continued to ignore geology. From 1900 to 1915 the significance of the relation of petroleum to anticlinal structure was clearly demonstrated for many areas by the investigations and publications of the Federal Geological Survey.

The number of geologists now serving the industry in the United States, in the employ of companies and in the employ of Governmental, State, and other institutions, appears to exceed 3,000—a num-

ber somewhat larger than the number of geologists in the United States who are members of the American Association of Petroleum Geologists. Altogether, 2,354 geologists living in the United States were members of this organization on March 1, 1938.

It is noteworthy that the States having the greatest oil production are the ones that have most oil geologists, as indicated by the membership of the American Association of Petroleum Geologists as of March 1, 1938.

Texas, ranking first in production—510,318,000 barrels of oil in 1937 has ..... 868 geologists
California, standing second—238,521,000 barrels of oil in 1937—has ..... 314 geologists
Oklahoma, standing third—228,839,000 barrels of oil in 1937—has ..... 430 geologists
Louisiana, standing fourth—90,924,000 barrels of oil in 1937—has ..... 124 geologists
Kansas, standing fifth—70,761,000 barrels of oil in 1937—has ..... 134 geologists

In these five States there is one geologist for every 600,000 barrels of oil produced in 1937.

METHODS EMPLOYED BY THE PETROLEUM GEOLOGIST

The oil geologist, in the application of his science to the recovery of petroleum, has a wide field of opportunity before him and he makes use of facts and conclusions from many phases of geology, including structure, stratigraphy, paleontology, sedimentary petrology, sedimentation, geomorphology, and metamorphism. In his search for, and his location of, oil deposits he has from time to time abandoned or modified old methods and has adopted new methods of exploration. The available time will not permit the presentation of a full list of these methods; it will permit no more than brief mention of some major developments during the present century. Important developments during the early years of the century were the adoption of the structure contour to portray the structural features of prospective or producing oil and gas areas and also the application of the plane table and alidade as instruments for determining accurately the altitudes of the "key beds" that were contoured.

Aeroplane photography, first employed during the World War, was utilized about 1920 by the oil geologist. Subsequently its utilization by Governmental agencies and by oil and other companies has increased rapidly, and at present about half the area of the United

States has been covered by aerial photographs. To the geologist such photographs record a wealth of essential details of geologic features that are not obtainable by any other method of mapping. As the years pass, he relies more and more on such pictures and employs fewer and fewer plane table maps.

Surface structural mapping reached its peak application between 1920 and 1925, and it has thus for many years occupied a place of decreasing importance in the search for new oil fields. This decline is attributable to the gradual decrease in number of favorable structural features that can be recognized by surface geologic mapping.

Core drilling for the determination of structure was introduced in the United States in 1919 and was employed on an extensive scale for many years in portions of the Mid-Continent region.

The microscopic examination of well cuttings was begun on a large scale in 1917 and since that time it has reached a place of fundamental importance. To it the oil geologist now gives about half of his effort. The practice of obtaining cores of oil sands and other important beds in order that their character may be accurately noted is used in all producing areas. The microscopic study of insoluble residues obtained by dissolving in hydrochloric acid well cuttings of limestones and dolomites was begun in 1924 by H. S. McQueen (9). It has been successfully utilized by the oil industry in the Mid-Continent region —from Ohio and Tennessee on the east to Kansas and New Mexico on the west—for the determination of underground stratigraphy and structure.

Micropaleontology, first introduced in universities and also by companies to a limited extent as early as 1919, became an integral part of the oil business in the United States in 1924.

Geophysical methods, magnetic, gravimetric, electrical, and seismic, are widely used in the United States by the oil industry as a means for locating and mapping buried structural features. The adoption of the seismograph followed the discovery of its applicability during the World War for locating long range guns. In its use by the oil industry the long range guns are replaced by explosive charges in prospective oil localities. The first applications of gravimetric methods in the detection of anticlinal structure in this country were made in 1917 and 1919 by the Coast and Geodetic Survey when stations on Damon Mound, Texas, and Paleozoic folds in Maryland were occupied at the request of David White of the Geological Survey (21). In 1924 oil companies located three salt domes by geophysical methods, the Nash dome by means of the torsion balance, the Orchard dome

by the seismograph, and the Long Point dome by both the torsion balance and the seismograph. Since 1924 a total of about 100 salt domes in the Gulf Coastal Plain and many other structural features from New York to California have been found by means of geophysical methods.

A type of well record or log, known as an electrical log, was developed in 1928. This type of well record is a great aid in exploratory drilling and the exploitation of oil fields. It shows the electrical resistivity and the relative porosity of the beds passed through by the drill. It permits the identification of oil- and water-bearing sands and gives useful information concerning the character of the beds. This information, in many areas, is more accurate than that provided by sets of cuttings.

PROGRESS OF PETROLEUM GEOLOGY

The progress of the science of petroleum geology is revealed in many publications, particularly those of the Federal and State Geological Surveys and the American Association of Petroleum Geologists. This Association was organized in Tulsa, Okla., in 1917 with a membership of 94 and now (December, 1938) has a domestic and foreign membership of about 3,000—a number greater than that of any other geological society in the world. The Association issues a monthly bulletin containing about 150 pages in each number, and in addition it has issued twelve special volumes. The reports of the Federal and State Geological Surveys dealing especially with petroleum geology are numerous and constitute a major portion of the literature on the subject.

An important factor in the development and progress of petroleum geology has been the mounting store of geologic data supplied by wells that have constantly increased both in number and depth. The number of wells that have been drilled for oil and gas in the United States exceeds 900,000. The world's deepest well, completed this year in the southern San Joaquin Valley, California, reached a depth of 15,004 feet. This well is nearly 9,000 feet deeper than the mine workings (slightly more than 6,150 feet) of the Quincy Mining Co., Hancock, Mich., and is about 6,500 feet greater than the 8,530-foot workings of one of the Crown Mines on the Rand. The producing zone of this deep California well is from 13,092 to 13,175 feet, but a more recently completed well of the Fohs Oil Co. in Terrebonne Parish, Louisiana, is producing from a slightly greater depth—namely, 13,254 to 13,266 feet.

CONTRIBUTIONS OF PETROLEUM GEOLOGY TO GENERAL SCIENCE OF GEOLOGY

Petroleum geology, because of its wide field of opportunity for the investigation of geologic conditions on the surface and also geologic conditions to the depths penetrated by wells—15,004 feet—and to the depths reached by geophysical methods—more than 30,000 feet—has made notable contributions to the general science of geology. Some of the more important contributions will be mentioned briefly.

Anticlines, as already noted, were first sought as favorable structural features on which to locate drilling sites for oil; but, with further drilling and the consequently increased knowledge of the occurrence of petroleum, it was learned that oil occurs not only on simple anticlines but also on many other types of structural features which include terraces, anticlinal noses, faults, unconformities, salt domes, lenticular sands, and buried hills.

Buried hills and the superposition of surface anticlines over them were brought to the attention of geologists by Sidney Powers (12) following the discovery of granite hills underneath the Eldorado line of folding in Kansas and of hills of Ordovician rocks underneath the Pennsylvanian sand production at Healdton, Okla.

Our knowledge of the geology of the salt domes in Louisiana and Texas has been revolutionized in the last quarter of a century. Now the domes are generally regarded as intrusive plugs of salt that moved upward from bedded salt of probable late Jurassic or early Cretaceous age. The salt is believed to have moved upward as much as 30,000 feet in the coastal portions of Louisiana and Texas. Formerly the salt masses were believed to have been formed as a result of volcanic activity, gas uplift, or the crystallization of the salt along zones of weakness in the rock strata.

The Gulf Coastal Plain may be cited as an example of an area whose tectonic map has undergone great transformation as the result of oil exploration. To the tectonic map of the Gulf Coastal Plain such structural trends as the Mexia fault zone, the buried course of the Ouachita belt of Paleozoic rocks, and the Gulf Coast geosyncline, have been added.

From the determination of the effect of regional structural deformation and the attendant metamorphism on deposits of petroleum and coal in the eastern United States David White drew, in 1915, a "deadline" beyond which oil may not be expected in the Appalachian and Ouachita regions (22). This oil "deadline," or extinction zone,

lies between the 60- and 65-isocarbs, lines connecting points where the coals have 60 to 65 per cent of fixed carbon.

Also, the composition of the hydrocarbon gases in the northern Appalachian region bears a close relation to the structure and the degree of metamorphism of the associated strata. This has been pointed out recently by S. H. Hamilton (6), Charles R. Fettke (4), Paul H. Price (13), and A. J. W. Headlee (13).

From the measurements of the temperatures of deep wells by Van Orstrand (20) and others in the United States it has been shown that relatively high temperatures are generally associated with faults, salt domes, sand lenses, and anticlines of both large and small closure. It appears that both the local and regional variations of earth temperatures of the sedimentary strata thus penetrated by wells are related to thermal conductivity and to the depth to the underlying crystalline basement. Differential uplift on either a large or a small scale would tend to elevate the isotherms irregularly.

Stratigraphy, of a refined character, has received impetus in consequence of the requirements of the oil industry for exact information concerning the thickness and character of the rock strata of prospective oil regions and of areas under development. This type of information is required for an interpretation of geologic history and for the preparation of precise structure maps. The geologic history has a bearing on the origin and migration of oil and the structure maps may reveal favorable places for its accumulation.

Time will permit mention of only three interesting types of stratigraphic work. One of these is to be found in western Kansas where petroleum geologists have matched the intervals between bentonite beds in the Niobrara chalk in a way suggestive of the matching of tree rings by archaeologists in dating ancient pueblos in New Mexico and Arizona. In this way the geologists obtain extremely accurate data for mapping structure on the surface and in core drilling.

An investigation by N. W. Bass (1) and his coworkers of the shoestring sand bodies that yield much petroleum in Greenwood and Butler Counties, Kansas, and Osage County, Oklahoma, has shown that these elongated lenticular sand bodies represent sand bars along ancient shore lines during the Pennsylvanian epoch. A study of 22,000 well logs in and near the oil fields supplemented by an investigation of nearly the full length of the Atlantic and Gulf Coasts has made possible the mapping of land features and shore lines of the ancient seas as they existed in Kansas and Oklahoma 250 million years ago.

The recognition and determination of changes in facies of sediments occupy the attention of all stratigraphic geologists. Many such changes may be noted in the exposed rock strata, as in the Permian section of Utah and in the Cretaceous section of the Book Cliffs of Colorado and Utah. The most striking and best known example of such facies changes in this country is offered by the Permian rocks of the Delaware Basin of New Mexico and Texas. The basin was surrounded by a reef zone, and this in turn by a back reef zone. Each of these—the basin and the two zones—is characterized by different kinds of deposits. These relations are exceptionally well displayed in the Glass and Guadalupe Mountains and also by the records of thousands of oil wells in the plains east of the mountains.

Stratigraphic information and also areal geologic maps have been contributed generously by oil companies to State and Federal Geological Surveys for use in connection with official investigations in the petroleum-producing States. The publication of such modern State geologic maps as those of Oklahoma (10), Kansas (11), and Texas (3) was greatly facilitated through the active interest and support of the petroleum geologists and companies in those States. The great stock of information acquired by oil companies in California has been drawn upon in large measure in the preparation of two recently issued volumes—one entitled *Geology of California*, by R. D. Reed (14) and the other *Structural evolution of California*, by R. D. Reed and J. S. Hollister (15).

The stratigraphic information supplied by the wells drilled for oil and gas enables the geologist to draw geologic maps of the past. Such maps are areal geologic maps and they thus differ from paleogeographic maps which show the distribution of land and water. An early, and perhaps the first, areal geologic map based almost entirely on well data was one for northeastern Oklahoma compiled by Luther H. White. It was published in 1926 by the *Oil and Gas Journal* (23) and also by the Oklahoma Geological Survey (23). More recently, such maps of Kansas (8), Oklahoma (8), Texas (16), and a large portion of the United States (7) have been published. The deep drilling for oil and gas provides not alone stratigraphic information but also structural data that permit the preparation of subsurface structure maps, both local and regional in character. In the words of R. A. Daly at the banquet of the Geological Society of America in Tulsa, Okla., on December 30, 1931, the petroleum industry has contributed the third dimension to geology.

DEEP DRILLING AND SEARCH FOR PETROLEUM DISCOVER OTHER MINERAL PRODUCTS

The petroleum industry, in its addition of this new dimension to geology, has had an unusual opportunity to discover mineral products that lie deep below the surface. Commercially important deposits of five mineral products thus discovered with the advent of deep drilling and search for petroleum are natural gas, helium, natural carbon dioxide, potash in New Mexico, and sulphur in the coastal areas of Louisiana and Texas. The five industries centering around these may thus be regarded as quintuplets of mother petroleum in the household of the mineral industry. A few vital and other statistics of interest about each of the quintuplets will be mentioned.

The commercial utilization of natural gas, one of our principal sources of light and power, dates back as early as 1821 when gas from a shallow well at Fredonia, New York, was used in homes in that village. Our present marketed output of natural gas, amounting in 1937 to 2,370 million cubic feet, comes from 24 States and is transported through 85,000 miles of trunk lines to consumers in 35 States. The known reserves of this convenient and efficient source of heat and energy are, according to R. W. Richards,[2] at least of the order of 100 trillion cubic feet.

Gas wells suitable for producing solid carbon dioxide, known generally as dry ice, have been drilled in Montana, Colorado, Utah, New Mexico, and California; and plants for the manufacture of dry ice from gas supplied by such wells have been constructed in recent years at Wellington, Utah, Witt and Bueyeros, N. Mex., and Niland, Calif. Dry ice is a convenient refrigerant and is being produced in increasing quantities, due in part to the growing demand for it by transcontinental and transoceanic shippers.

Sulphur was discovered on a salt dome at Sulphur, La., in 1865 by the Louisiana Petroleum & Coal Co. while prospecting for oil. Sulphur production was begun in Louisiana in 1903. To January 1, 1938, 41,163,000 long tons of sulphur valued at over three-quarters of a billion dollars has been produced from the cap rock of salt domes on the Gulf Coast of Louisiana and Texas. Before the development of the Louisiana and Texas deposits 95 per cent of the world's supply of sulphur came from Sicily. At present these two States supply the greater part of the world's sulphur and more than 99 per cent of the domestic output.

[2] Personal communication.

The United States possesses the only known natural gas fields in the world that yield gas sufficiently rich in helium to warrant the extraction of this element on a commercial scale. The richest helium-bearing gases, those containing 1 to 8 per cent, are found in southeastern Kansas, southeastern Colorado, eastern Utah, and in the Texas Panhandle. The production of helium on a large scale was born of the necessity to find during the World War a non-inflammable substitute for the extremely inflammable hydrogen gas in balloons and dirigibles. The operation of experimental plants in Texas and Canada, beginning in 1918, led to the erection in 1919 of a production plant at Fort Worth, Texas, and later other plants, one by the Helium Company at Dexter, Kans., in 1927, and the other by the Bureau of Mines near Amarillo, Texas, in 1928.

American potash, like our helium, was first produced during the World War and it now supplies a major portion of our domestic requirements. An energetic search for possible sources of potash in this country began in 1911. One of the possible sources thus investigated was the Permian salt of Texas and New Mexico. Information about the extent and character of the potash deposits in these States acquired from oil company wells and from Government and private core tests revealed commercial deposits of potash in New Mexico. Shipments began in 1931 and they totaled 700,000 tons of crude potash salts in 1937.

PETROLEUM RESERVES OF UNITED STATES

Our petroleum reserves, because of the nature of the occurrence of petroleum, are imperfectly known. Petroleum is a liquid contained in the rocks deep below the surface in many small widely scattered areas. It is discovered by the driller who is aided in his search by the accumulated knowledge about oil and its occurrence.

A number of estimates of the total petroleum resources of the United States were prepared between 1909 and 1921. During this period, however, it became evident that the unproved reserves in unknown fields awaiting future discovery could not be estimated with any degree of accuracy whereas the quantity of oil in the proved reserves, recoverable by then current methods of production, could be estimated with reasonable accuracy on the basis of the past production experience of depleted fields. The first estimate in which the proved reserves were separated from estimates of undiscovered fields was made in 1921 by the Geological Survey with the cooperation of the American Association of Petroleum Geologists. In this estimate

5 billion barrels were classified as oil "in sight" on January 1, 1922, and 4 billion barrels additional as "prospective and possible" and recoverable by current methods of production (18). A number of estimates have been prepared since 1921.

The individual estimates of the petroleum reserves that have been made in 1921 and subsequent years differ somewhat but they all possess a similar order of magnitude. Since 1930 the estimates of proved reserves have ranged from 10 to 15.8 billion barrels.

The proved reserves in the ground, like the stocks of petroleum held above ground, are constantly changing in quantity. They are depleted by the output of producing wells and increased by the discovery of new fields and deeper pools. During the period 1922 to 1938 for which figures of proved reserves are available many large fields were discovered so that, notwithstanding the consequent greatly augmented production, the proved reserves have increased.

FUTURE PETROLEUM SUPPLY OF UNITED STATES

The continued discovery of new fields and deeper oil-bearing zones is required to meet future demands, just as it has since the beginning of the industry in the United States. The extent to which new sources of supply are discovered and produced depends upon the payment of such prices by the consumer as will permit the industry to carry the heavy and increasing expense of new exploration and maintain profits.

Much oil remains to be discovered in new fields and in deeper pools, but the exact location of these fields and the quantity of petroleum they will yield are not known; they will not be known in advance of drilling. Nevertheless, their number, whatever it may be, is definitely limited and each newly-found field leaves one less to be discovered.

The answer to the question "When will the day of petroleum shortage in the United States be reached?" lies not alone in the supply of oil remaining in the ground. It rests also with the geologist to continue to aid in the increasingly difficult problem of discovery, with the engineer to improve drilling technique and to increase recoveries, and with the chemist to continue improvements in refining practice. In part, it rests on the price that the public can pay in the future for oil products, and that in turn depends in part on increased efficiency in use. In a large measure it rests on conservation and efficiency in the discovery, development, and production of our future oil fields.

The future undoubtedly will see continued advances in science and technology affecting the discovery, recovery, refining, and utilization

of petroleum. Thus far, these advances have enabled us to keep supplies ahead of needs, but they afford us no assurance that the same record can be maintained indefinitely.

In this connection it is of interest to call attention to some of the concrete accomplishments of recent years. The recovery of gasoline from a barrel of oil has more than trebled in the last 40 years—from about 5½ gallons in 1899 to about 18½ gallons in 1937. In the 15-year period from 1922 to the end of 1936 the geologist and the petroleum engineer have aided the driller in the addition of 10.8 billion barrels to our petroleum reserves, despite the production of 12.8 billion barrels during that period. Also, from 1920 to the end of 1936 the chemist by the introduction and improvement of cracking processes, has conserved 8.5 billion barrels of crude oil (19). The petroleum engineer is meeting energetically the challenge to recover the 65 to 85 per cent of oil remaining in the ground after a field no longer yields oil by the older methods of production. Each year witnesses the improvement and extension of recovery methods, such as acid treatment and repressuring by the introduction of gas, air, and water into the oil-bearing zones. The increased adoption and refinement of such methods in areas where geologic and other conditions permit their use will lead to the recovery in places of 50 per cent or more of the total oil content of the producing zone.

Moreover, when a shortage of domestic crude petroleum arrives and there is a consequent rise in prices of petroleum products, substitutes will be drawn upon just as they are now drawn upon to some extent in some countries that are supplied with little or no oil resources. Some of these substitutes are oil products from coal and oil shale, alcohol from farm products, and gases from wood. Our future resources of coal and oil shale have been so determined by geologic evidence and exploration that we know their approximate extent and quantity. According to Dean E. Winchester (24), the oil shale deposits of the United States will yield 92,144,935,000 barrels of oil, if and when the price of oil permits. Should coal be called upon to supply the demands now met by oil and gas, the coal reserves of the United States would, according to independent estimates by T. A. Hendricks[3] and Arno C. Fieldner (5), last about 2,000 years. These two estimates are based on the assumption that the consumption of energy from mineral fuels will equal the maximum rate of consumption in the past (approximately 23,400 trillion B.t.u. in 1929) and

[3] Personal communication.

also are based on the assumption of a 30 per cent loss of coal in mining. Concerning the cost of motor fuel substitutes, Doctor Fieldner (5) comments as follows:

Reliable information on the cost of making gasoline from coal in British and German plants is not available, but it is believed that it is three or four times the present cost of producing gasoline from petroleum in the United States. These costs will be reduced by further research, but no other liquid motor fuel, whether it be from coal, oil shale, or vegetable matter, can hope to be as cheap as our present petroleum fuels.

The following significant statement on this subject is contained in a recent press memorandum of the Department of the Interior relative to the work of the Bureau of Mines (Oct. 24, 1938):

By the time that depletion of our petroleum resources reaches the point when a motorized Nation must begin to look to other sources for some of its fuel, it is hoped that motor fuel can be supplied from coal so efficiently and cheaply that the transfer can be made from the old fuel to the new without drastic adjustments.

LITERATURE CITED

1. BASS, N. W. *Origin of Bartlesville shoestring sands, Greenwood and Butler Counties, Kansas.* Am. Assoc. Petroleum Geologists Bull. **18**(10): 1313–1345. October, 1934.
   —— *Origin of the shoestring sands of Greenwood and Butler Counties, Kansas.* State Geol. Survey of Kansas Bull. **23**. 1936.
   —— CONSTANCE LEATHEROCK, W. REESE DILLARD and LUTHER E. KENNEDY. *Origin and distribution of Bartlesville and Burbank shoestring oil sands in parts of Oklahoma and Kansas.* Am. Assoc. Petroleum Geologists Bull. **21**(1): 30–66. January, 1937.
2. CADMAN OF SILVERDALE, THE RT. HON. LORD. Foreword, *The science of petroleum.* **1**. Oxford University Press. 1938.
3. DARTON, N. H., L. W. STEPHENSON, and JULIA GARDNER. *Geologic map of Texas.* U. S. Geol. Survey. 1937.
4. FETTKE, CHARLES R. *Oriskany as a source of gas and oil in Pennsylvania and adjacent areas.* Am. Assoc. Petroleum Geologists Bull. **22**(3): 241–266. March, 1938.
5. FIELDNER, ARNO C. *Fuels of today and tomorrow.* Am. Soc. for Testing Materials, Proc. **37**(1). 1937.
6. HAMILTON, S. H. *Oriskany explorations in Pennsylvania and New York.* Am. Assoc. Petroleum Geologists Bull. **21**(12): 1582–1591. December, 1937.
7. LEVORSEN, A. I. *Studies in Paleogeology.* Am. Assoc. Petroleum Geologists Bull. **17**(9): 1107–1132. September, 1933.
8. MCCLELLAN, HUGH W. *Subsurface distribution of pre-Mississippian rocks of Kansas and Oklahoma.* Am. Assoc. Petroleum Geologists Bull. **14**(12): 1535–1556. December, 1930.
9. MCQUEEN, H. S. *Insoluble residues as a guide in stratigraphic studies.* Missouri Bureau of Geology and Mines 56th Biennial Report, Appendix I. 1931.
10. MISER, H. D. *Geologic map of Oklahoma.* U. S. Geol. Survey. 1926.
11. MOORE, RAYMOND C. and KENNETH K. LANDES. *Geologic map of Kansas.* State Geol. Survey of Kansas. 1937.
12. POWERS, SIDNEY. *Granite in Kansas.* Am. Jour. Science. **44**(4): 146–150. 1917.
    —— *The Healdton oil field, Oklahoma.* Economic Geology. **12**: 594–606. 1917.
    —— *Reflected buried hills and their importance in petroleum geology.* Economic Geology. **17**: 233–259. 1922.
    —— *Reflected buried hills in the oil fields of Persia, Egypt, and Mexico.* Am. Assoc. Petroleum Geologists Bull. **10**(4): 422–442. April, 1926.
13. PRICE, PAUL H. and A. J. W. HEADLEE. *Regional variations in composition of natural gas in Appalachian province.* Am. Assoc. Petroleum Geologists Bull. **22**(9): 1153–1183. September, 1938.

14. REED, RALPH D. *Geology of California.* Am. Assoc. Petroleum Geologists. Tulsa, Oklahoma. 1933.
15. —— and J. S. HOLLISTER. *Structural evolution of southern California.* Am. Assoc. Petroleum Geologists, Tulsa, Okla. 1936.
16. SELLARDS, E. H. Maps showing distribution of Upper Cambrian, Lower, Middle, and Upper Ordovician, Silurian, and Devonian in Texas. Advance prints from *Geology of Texas,* IV. *Petroleum Resources.* Univ. of Texas, Bureau of Economic Geology. April, 1938.
17. TEAGLE, W. C. Foreword, *The science of petroleum.* 1. Oxford University Press. 1938.
18. UNITED STATES GEOLOGICAL SURVEY. *The oil supply of the United States.* Amer. Assoc. Petroleum Geologists Bull. 6(1): 42–46. 1922.
19. VAN COVERN, FRED. *Status and outlook of petroleum supply, demand, and stocks.* Am. Petroleum Inst. Quart. 7(2): 9. April, 1937.
20. VAN ORSTRAND, C. E. *Some possible applications of geothermics to geology.* Am. Assoc. Petroleum Geologists Bull. 18(1): 13–38. January, 1934.
—— *Temperature gradients.* In *Problems of Petroleum Geology.* Pp. 989–1021, Am. Assoc. Petroleum Geologists, Tulsa, Okla. 1934.
21. WHITE, DAVID. *Gravity observations from the standpoint of the local geology.* Geol. Soc. of America Bull. 35(2): 207–277. June 30, 1924.
22. —— *Some relations in origin between coal and petroleum.* This JOURNAL 5: 189–212. March 19, 1915.
—— *Metamorphism of organic sediments and derived oils.* Am. Assoc. Petroleum Geologists Bull. 19(5): 589–617. May, 1935.
23. WHITE, LUTHER H. *Oklahoma's deep horizons correlated.* Oil and Gas Jour. 24(45). April 1, 1926.
—— *Oil and gas in Oklahoma: subsurface distribution and correlation of the pre-Chattanooga ("Wilcox" sand) series of northeastern Oklahoma.* Oklahoma Geol. Survey Bull. 40-B. 1926.
24. WINCHESTER, DEAN E. *The oil possibilities of the oil shales of the United States.* Report II of the Federal Oil Conservation Board to the President of the United States, pp. 13–14. 1928.

PALEONTOLOGY.—*The crossopterygian hyomandibular and the tetrapod stapes.*[1]

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Romer's description, in 1937, of the braincase of *Megalichthys,* a Permo-Carboniferous crossopterygian fish, showed that the hyomandibular bone articulated with the otic region by two heads, one dorsal and one ventral to the jugular vein. This arrangement, elsewhere unknown in vertebrates, had been anticipated in part by Schmalhausen, DeBeer and Watson. They could not, however, attribute the two-headed hyomandibular to any particular fish, and their hypotheses differed greatly in details. The views of Schmalhausen and DeBeer were summarized by Goodrich (1930) in his *Studies on the structure and development of vertebrates,* and those of DeBeer again by Romer (1937). Watson's related suggestion is in his paper on the origin of Amphibia (1926).

In the summer of 1937 I had the privilege of studying the *Megalichthys* material with Dr. Romer and attempting to restore some of

[1] Presented before the Vertebrate Section of the Paleontological Society on December 29, 1938. Received December 29, 1938.

the soft anatomy. This paper presents two suggestions: (1) That the articulations of the hyomandibular are carried over essentially unchanged, and may be identified, in the connections of the stapes with other skeletal parts in most tetrapods, and (2) that the stapedial muscle is not limited to mammals but probably came up in their ancestry from the anterior edge of the levator hyoidei of fishes. Most of the data are from published sources, but I have added to them a series of simple reconstructions and two or three new observations.

Figure 1 is a diagrammatic reconstruction of the hyomandibular of *Megalichthys* and its relations to other parts. The attachments to skeletal parts are numbered arbitrarily: 1 the dorsal process, to the parotic region of the cranium above the jugular canal, 2 the ventral or otic process, below the jugular canal, 3 the connection with the ceratohyal, 4 that with the quadrate, and 5 with the operculum. The latter two connections are not represented by distinct processes, but were undoubtedly present as close attachments in all generalized hyostylic operculate fishes. Above the groove for the jugular vein, on the posterior part of the otic region, is a smooth muscle scar, which could only be for the levator hyoidei, likewise present in generalized hyostylic fishes. Whether this muscle extended as far down as the mandible is not determined, so that its restoration is conservative. In Amphibia, however, the levator hyoidei is largely converted into the depressor mandibulae by shifting its insertion to the posterior end of the lower jaw.

Three brief comparisons with the arrangement in other fishes will show that this type of hyomandibular occupies, probably, a fairly central, primitive position in the evolutionary scheme. Figure 2 indicates the corresponding structures in a dissection of *Squalus*, a shark. The articulation with the cranium is single and ventral to the jugular vein. Probably it is equivalent to no. 2, and no. 1 is either primitively or secondarily absent. No. 5 probably never existed, as there is no evidence that sharks ever had a bony operculum.

In the advanced fishes, Actinopteri, the hyomandibular articulates with the braincase above the jugular vein instead of below, and presumably articulation 2 has been lost, on the assumption that the double-headed hyomandibular is ancestral for these fishes. Numbers 3, 4 and 5 are, of course, regularly present.

The Dipnoi, lungfishes, make a more difficult problem, as the hyomandibular is so far reduced as to be almost unrecognizable in the adult, and has lost practically all its primitive connections. But even here, in the embryo of *Neoceratodus* (Fig. 3), we may possibly see a

remnant of a double cranial attachment with the jugular vein between, and also one to the quadrate and another for the ceratohyal. If this be the correct interpretation, the only one of our five connections actually missing is that for the operculum. In modern Dipnoi, at least, the operculum is greatly reduced and depends primarily upon its extensive muscle sheet for support.

Enough has been said to show that Romer's discovery may be the

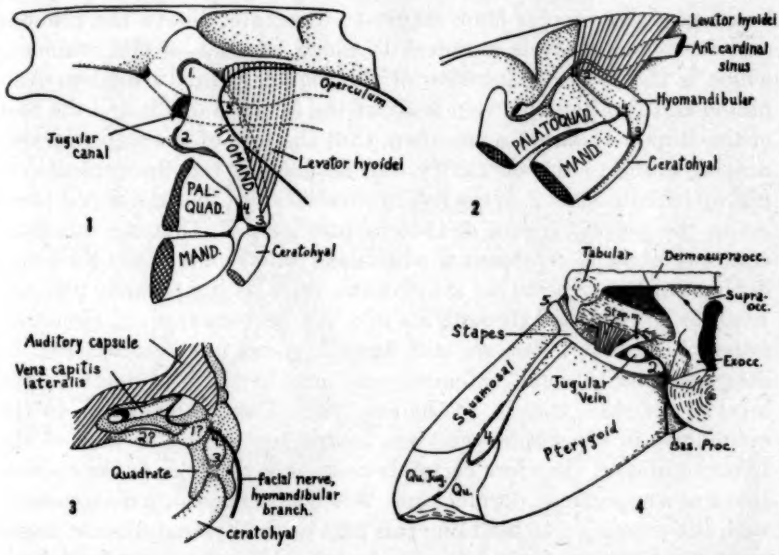

Fig. 1.—Crossopterygii: *Megalichthys*. (Adapted after Romer, 1937.) Left lateral view. Fig. 2.—Elasmobranchii: *Squalus*. Left lateral view. Fig. 3.—Dipnoi: *Neoceratodus*, embryo, 18.5 mm. (Modified after Goodrich, 1930.) Posterior view, right side. Fig. 4.—Embolomeri: *Orthosaurus*. (Based on Watson, 1926.) Posterior view, left side.

means of settling the long dispute over homologies of the hyomandibular and its cranial articulations in fishes. Turning back to *Megalichthys* again, the prevailing opinion for some years has been that Crossopterygii stand very close to the ancestry of tetrapods, and it should be profitable to make as detailed a comparison as possible between the hyomandibular and the amphibian stapes.

Figure 4 is a composite reconstruction of the stapes in the embolomerous Stegocephalia, based partly on Watson's figures and partly on his descriptions (1926). On the lower portion of the otic capsule the foot of the stapes rested in a pit, which, however, did not pene-

trate the capsule wall. He calls it the pseudofenestra ovalis. It is clearly an early stage in the evolution of a complete fenestra into the otic cavity, but presumably sound could already be transmitted by way of the stapes. Watson says he believes a dorsal process to have been present in Embolomeri, and also one to the quadrate, both of them doubtless cartilaginous. There is a small pit on the quadrate, sometimes at the point where the squamosal, pterygoid and quadrate meet (*Orthosaurus*), facing towards the otic capsule, and showing the location of the process from stapes to quadrate. Above the pseudofenestra ovalis there is a concavity along the side of the braincase which is the probable location of the jugular vein. In modern Amphibia and Reptiles this vein is above the fenestra ovalis and the foot of the stapes. It would seem, then, that the foot of the stapes, transmitting sound to the ear cavity, can be nothing but the ventral cranial articulation, no. 2, of the fish hyomandibular; that the dorsal process to the parotic region of the cranium is no. 1; that the quadrate connection, no. 4, is present as a cartilage rod in some cases. No doubt during ontogeny the hyoid attachment, no. 3, is temporarily present; whether it continued through life in a ligamentous form is, of course, impossible to say. But we still have one end unaccounted for. In Stegocephalia this end extended outwards in the otic notch to the level of the skin, that is, to the ear drum. Connection no. 5, to the operculum in Crossopterygii, was located on the outer face of the hyomandibular, therefore certainly nearest to the skin, as the operculum was a superficial, dermal bone. When the operculum disappeared, with the transition to land life, this part of the hyomandibular might most readily have been left attached to the integument and have served to receive sound vibrations from outside, while that area of the integument became the ear drum. Watson remarks that the bony stapes of Embolomeri seems to lie at right angles to that of, for instance, *Osteolepis*, the Crossopterygian which he used for comparison. We can see that this is not so much a shifting of position of the bone as the development of a new axis, namely from the fenestra ovalis to the otic notch instead of from the parotic process to the ceratohyal.

The bulk of the levator hyoidei muscle of Crossopterygii had, with the reduction of the hyomandibular, changed its insertion to the mandible, being known from now on as the depressor mandibulae. But there can be little question, on the basis of evidence from certain reptiles and from mammals, that in early Stegocephalia a slip of this muscle continued to insert on the stapes, its origin being somewhere close to the parotic process and its course being external to the jugu-

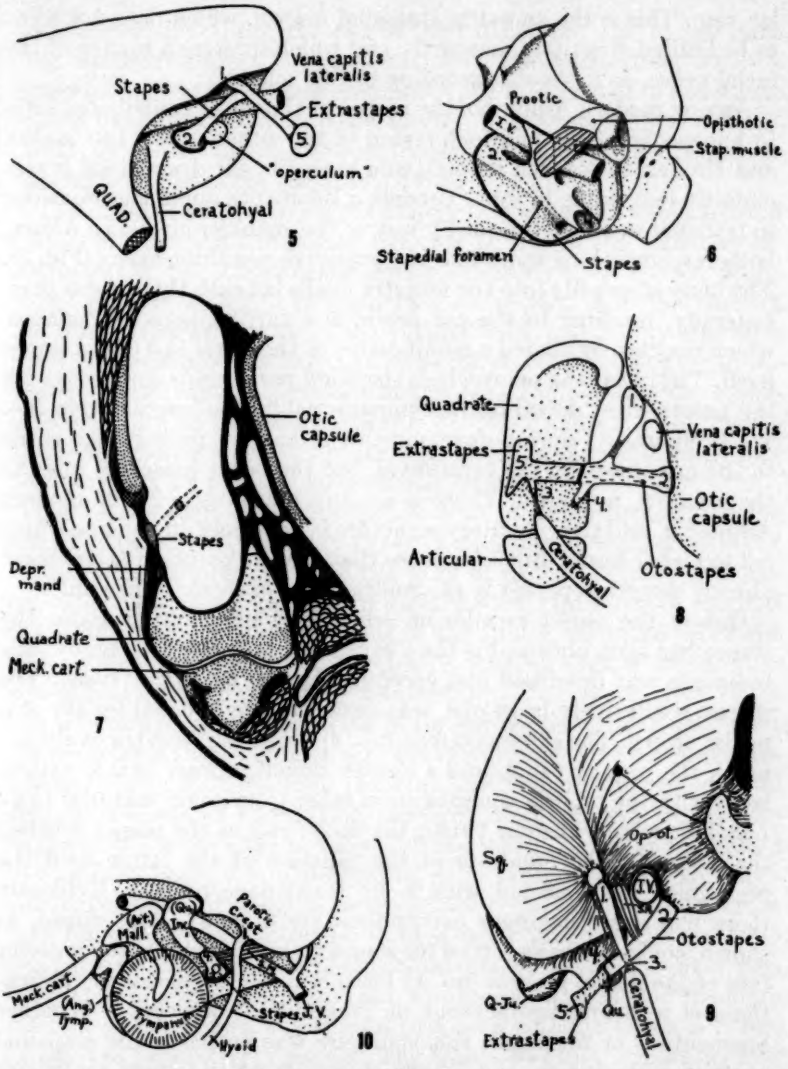

Fig. 5.—Anura: *Rana catesbeiana*. Left lateral view. Fig 6.—Cotylosauria: *Captorhinus*. (Adapted after Price, 1935.) Left lateral view. Fig. 7.—Chelonia: *Chrysemys marginata*. (Just hatched, C. L. 25 mm.) Left otic capsule, transverse section. Fig. 8. —Lacertilia. Generalized diagram. Posterior view, left side. Fig. 9.—Theriodonta: *Kannemeyeria*. (Adapted from Pearson, 1924.) Posterior view left side. Fig. 10.—Marsupial embryo. Generalized diagram. Left lateral view.

lar vein. This is the ancestral stapedial muscle, which does not seem to be limited strictly to mammals, and which receives a branch of the facial nerve, as it should according to this scheme.

Among modern Amphibia the stapes of the adult contributes little to knowledge of the auditory region of any other types. In Caecilia and Urodela it is much reduced and even the ear drum itself is secondarily lost, while in some Urodela a substitute apparatus develops to transmit sound to the ear by way of the shoulder girdle. In Anura, however, something more like the primitive condition exists (Fig. 5). The bony stapes fits into the fenestra ovalis beneath the jugular vein. Laterally, reaching to the ear drum, is a cartilaginous extrastapes, which may be considered a modification of the distal end of the stapes itself. This, near the point where the bony part begins, connects with the parotic crest dorsal to the tympanic cavity and jugular vein (no. 1). Temporarily, during development, strands of procartilage reach to the quadrate and the ceratohyal, but the latter presently fuses to the cranium, as shown. There is no stapedial muscle in the modern Amphibia, and their auditory structure is definitely off the line which led to higher forms. But we can see that the five points of attachment already described persist in the Anura, three of them in the adult.

One of the oldest reptiles on which any information about the stapes has been obtained is the Cotylosaur *Captorhinus* (Fig. 6). The braincase was described and carefully figured by Price (1935). The stapes, a relatively large one, was perforated by a canal for the stapedial artery. The expanded foot (no. 2) fitted the fenestra ovalis beneath the jugular canal, and a slender dorsal process (no. 1) articulated with the prootic. Judging from other Cotylosaur material (e.g., *Labidosaurus*, Williston, 1910), the distal end of the stapes reached the corner of the quadrate at the junction of the latter with the pterygoid, or connected with it by a cartilage process. Evidently there was a cartilaginous extrastapes, for otherwise the stapes, as shown, could not have served for sound transmission. On the anterior face of the dorsal process (no. 1) Price found in *Captorhinus* "indications of a strong ligamentous or muscular attachment." Whether ligamentous or muscular, this structure was probably the stapedial muscle or its vestige, and I have shown its possible position in this figure.

An interesting bit of evidence on the stapedial muscle occurs in embryo turtles, for example in *Chelydra* and in *Chrysemys* (Fig. 7). A section made through the tympanic region of the latter at the time of hatching shows the anterior edge of the depressor mandibulae mus-

cle attached directly to the end of the extrastapes, but at the same time continuing down to the lower jaw. This connection, which I would interpret as a passing remnant of the attachment of a separate muscle to the stapes, disappears shortly, but is represented in adult turtles by a short ligamentous connection of the depressor muscle to the cartilage rim of the ear drum cavity.

The condition in some lizards closely resembles our reconstructed Stegocephalian and Cotylosaur ear, and all five of the primitive attachments of the stapes occur during ontogeny (Fig. 8). No. 1, the dorsal process, develops in temporary connection with the body of the stapes, lies externally to the jugular vein, and finally separates as an "intercalary" cartilage. An opposite process (no. 4) goes to the quadrate and usually persists through life. Temporarily the stapes is connected with the ceratohyal (no. 3). No. 2 and no. 5 are present as the functional inner and outer ends of the stapes, just as in Embolomeri, but no. 5 is cartilaginous (an extrastapes).

Before considering the somewhat more difficult problem of the mammalian ear it is necessary to try restoring the complete stapes of a Theriodont, if possible, from the work of Broom, Watson and others. Since very few of the known mammal-like reptiles have much of the auditory apparatus remaining in the fossils, we must select one which happens to show it most clearly, without regard for the particular line which may lead to mammals.

A diagram of an occipital view of the ear region in the Anomodont *Kannemeyeria* (based on Pearson, 1924) will suggest two or three important changes which took place as the mammalian ear evolved (Fig. 9). The stapes was a short, bony rod reaching from the fenestra ovalis to the inner edge of the quadrate, where its distal end rested in a groove. There was undoubtedly, as in other reptiles, a cartilaginous extrastapes, although it need not have been long, for the ear drum may have been slightly sunken into a canal already. The quadrate itself was in the process of reduction and formed only the inner portion of the jaw articulating surface. The fenestra ovalis, and therefore the foot of the stapes, was ventral to a deep notch in which it is safe to say the jugular vein passed. The whole auditory apparatus had come farther ventrad and mediad than in amphibians or other reptiles. There is a distinct parotic process on the border between the squamosal and opisthotic. Lateral to this, on the squamosal, was a broad trough providing an origin for the depressor mandibulae. Considering that the parotic process in earlier types receives articulation no. 1 (the dorsal process) from the stapes, and that it is external to

the jugular notch, I think that we may look for a homologous structure to attach to the same place in some of the mammal-like reptiles, that is, a dorsal process from the stapes or its equivalent. We may also suspect that the stapedial muscle originated on the face of the opisthotic just inward from the parotic process.

If the interpretation is correct so far it should not be too great a jump to the stapes of a primitive mammal in an embryonic stage (Fig. 10). The dorsal end of the hyoid arch becomes attached very early to the parotic crest dorso-laterally from the stapes proper, and externally to the jugular vein. This end of the hyoid is then called laterohyal or stylohyal. Goodrich (1930) noted its similarity to the dorsal process of reptiles. I suggest that this dorsal process of the reptilian stapes has detached itself, during the early evolution of mammals, from the remaining portion of the stapes, and associated with the hyoid alone (connection no. 3). It is possible, then, that in *Kannemeyeria* and its relatives the dorsal process was already becoming a so-called "stylohyal" and supported the ceratohyal directly, while the inner part of the stapes, with its extrastapedial, was more completely freed for auditory transmission. The stapes of mammals has lost the extrastapedial because the quadrate and articular moved into the ear cavity and took its place. The stapedial muscle, becoming almost microscopically small, is still associated in mammals with the auditory stapes proper.

The associations of parts, then, in the mammalian ear, are new, but the old morphological features of reptiles, amphibians and even fishes are still there and may be recognized, according to this theory. It may be that with the evolution of a mammalian larynx, and mobile muscular tongue, along with chewing movements of the lower jaw, there was reason for a more sturdy attachment of the hyoid arch to the cranium, and the most convenient method of obtaining it was by annexing the dorsal process of the stapes. At the same time the remainder of the stapes came to depend on the quadrate, while the latter was still in the upper jaw, for a more complete support than it had in amphibians or most reptiles, and thus drew closer the original attachment no. 4. At some time, as Broom pointed out (1912), there must have been a double articulation between the mandible and the upper jaw, consisting not only of the old joint between the quadrate and articular but of a new one between squamosal and dentary. In time the latter survived, while the quadrate and articular, being very close against the ear drum, were drawn into the auditory complex and replaced the old cartilaginous extrastapes.

Summary.—The crossopterygian hyomandibular bone, evolving into the tetrapod stapes, retains its original morphological relations largely unchanged, even to mammals. New functions and new locations of parts appear, but the connections, I suggest, remain essentially as follows: 1. The dorsal cranial head of the hyomandibular becomes the dorsal process of the stapes, and, in mammals, the so-called stylohyal. 2. The ventral head of the hyomandibular, below the jugular vein, becomes the foot of the stapes and occupies the fenestra ovalis. 3. The connection of the hyomandibular with the ceratohyal generally does not persist beyond early developmental stages in tetrapods, but apparently in the line leading to mammals the ceratohyal was still able to link itself to the cranium through the dorsal process of the stapes. 4. In many types the attachment to the quadrate disappears except in early development, but it was shown to be present in early Stegocephalians, Cotylosaurs, lizards and the mammal-like reptiles, while in mammals it becomes the joint between the stapes and the incus. 5. The attachment of the hyomandibular to the operculum in fishes seems to furnish a convenient point for that between the stapes and ear drum in early tetrapods. Later this end of the stapes became cartilaginous and was finally atrophied in the transition from reptiles to mammals.

The levator hyoidei muscle became split, in Amphibia, into a large depressor mandibulae and a small stapedial muscle, the latter probably being limited to certain Stegocephalia. Traces of the stapedial appear in some primitive reptiles, and in mammals it is regularly present, while the depressor mandibulae serves the Amphibia, reptiles and birds, but in mammals is replaced by the digastric.

LITERATURE CITED

BROOM, R. *On the structure of the internal ear and the relations of the basicranial nerves in* Dicynodon, *and on the homology of the mammalian auditory ossicles.* Proc. Zool. Soc. London, 1912, 419–426, 1 pl., 1 text-fig.

—— *The mammal-like reptiles of South Africa and the origin of mammals.* Witherby, London. 1932.

GOODRICH, E. S. *Studies on the structure and development of vertebrates.* Macmillan, London. 1930.

PEARSON, H. S. *The skull of the Dicynodont reptile* Kannemeyeria. Proc. Zool. Soc. London, 1924, 793–826, 18 figs.

PRICE, L. I. *Notes on the braincase of* Captorhinus. Proc. Boston Soc. Nat. Hist. **40**: 377–386, pl. 6–9. 1935.

ROMER, A. S. *The braincase of the Carboniferous crossopterygian* Megalichthys nitidus. Bull. Mus. Comp. Zool. **82**(1): 1–73, 16 figs. 1937.

WATSON, D. M. S. *The evolution and origin of Amphibia.* Phil. Trans. Roy. Soc. **214**(B): 189–257, 39 figs. 1926.

WILLISTON, S. W. *The skull of* Labidosaurus. Amer. Jour. Anat. **10**: 69–84, pls. i–iii. 1910.

EVOLUTION.—*The course of evolution.*[1] ROBERT F. GRIGGS, George Washington University.

To evince an interest in orthogenesis or even to recognize that it is entitled to serious consideration by a scientific society is perhaps a somewhat dangerous admission. For many biologists consider orthogenesis a relic of the mystical childhood of evolutionary doctrine quite of a piece with the transmission of acquired characters and scarcely to be mentioned in a respectable Society. One authority expresses the feeling of many when he bluntly calls orthogenesis an "anachronism." Altenburg holds that "The theory of orthogenesis depends for its acceptance not so much on our knowledge of certain facts as it does on our ignorance of them."[2]

Yet the officers of the Paleontological Society ask me to open a discussion of the subject; because, in the words of their invitation, "The consideration of orthogenesis by the Society several years ago did not clarify the subject."

This statement again is an admission, at least that the subject is difficult to clarify. What chance is there of reaching a clearer understanding this time than on the previous occasion?

IS ORTHOGENESIS ESSENTIALLY MYSTICAL?

The zoologists' objections to orthogenesis so cogently set forth during the earlier discussion by Dr. Friedmann boil down, I believe, to the supposition that orthogenesis is essentially a mystical interpretation of evolution which calls into play not only unknown but unknowable agencies which are beyond the reach of scientific inquiry, that orthogenesis is really a Doctrine of Faith rather than a Law of Science. In so far as this is correct, the subject is certainly out of reach of scientific discussion; and if this be the whole truth, we can no more hope to reach a decision on orthogenesis than we could on one of the questions debated by the old Scholastics.

But if orthogenesis were, wholly outside the realm of evidence, it would in these modern days no longer constitute any problem at all. Its difficulty lies exactly in the fact that both natural and supernatural considerations have entered into its discussion. The problem is then to disentangle these elements. Needless to say, I shall not attempt to consider the mystical elements—not because I disbelieve in a theistic universe but because as I have said, that is a matter for

[1] Presented before the Paleontological Society of Washington at a symposium on orthogenesis, November 16, 1938. Received December 14, 1938.

[2] ALTENBURG, EDGAR. *How we inherit.* P. 120. 1928.

faith and is not susceptible of proof or disproof by scientific methods.

As in any controverted subject, we may well begin with a definition. Is it correct to state that the essential feature of orthogenesis is that it holds that evolution proceeds in definite directions rather than at random—that the course of evolution follows definite trends? And further it is usually held, I believe, that the tendency to fall into such definitie lines of evolution is characteristic of the nature of protoplasm itself. Other elements which have entered into the conception are, I think, mostly concerned with external causes of the trends and are, in the absence of any real understanding of such causes, mystical, or, to say the least, highly speculative.

Observers are not wanting, however, who strike at the very idea of evolutionary trends quite apart from any considerations as to cause. Altenburg says flatly that orthogenesis "contradicts all that we know about mutations, especially as shown by the careful studies made on the insect *Drosophila*," and again, "The mutation theory also makes untenable the theory of orthogenesis, according to which changes take place along predetermined lines and not in all directions as demanded by the mutation theory."

Here we have clearly set down the divergence in philosophy that has arrayed biologists in two hostile camps, the one dominated by the zoologists and the other by the paleontologists.

Is evolution haphazard, produced by mutations which occur in a miraculous manner, essentially supernatural in that they are caused by circumstances entirely outside of the ordinary run of nature? In this view, the only means by which the orderly relationships which we observe throughout nature could be produced is by natural selection. The adherents of such a theory account for the steady progress of the Equidae from a primitive five-toed ancestry down to the single-hoofed horses of today by the natural selection of random mutations alone. This theory would seem to me to put its adherents under a serious disadvantage at the start by imposing on them the necessity of proving that at every step in the evolution of the horse each slight decrease in the size of the lateral toes was an advantage great enough to favor in the struggle for existence those individuals which possessed it over those which did not.

Not all the geneticists, even though they have no use for orthogenesis, adopt this extreme view. Newman[3] states a very much stronger and I believe more generally held position when he writes, "It should be said that definitely directed evolution is now believed

[3] NEWMAN, H. N. *Readings in Evolution.* 3rd ed., p. 36.

to be one of the laws of organic evolution but we have no clear ideas as yet as to what are its underlying causes. Therefore *orthogenesis is not a causo-mechanical theory of evolution at all.*" (Italics in original.) Having thus delivered themselves, the geneticists smugly withdraw to their milk bottles to nurse their *Drosophila* and the paleontologists may throw as many of their figured stones at them as they please without in the least disturbing their self-satisfied self-sufficiency.

If the attitude of the unorthogenetic brethren were entirely snobbery, it would not last long and we would not need to concern ourselves with it. The truth is, however, that they have opened up a serious weakness in the orthogenetic position. In the minds of many men, the theory of orthogenesis shares with the so-called theory of special creation the onus of being merely a pseudo-explanation of the facts with which it deals. They hold that it substitutes a name for an explanation and really carries its adherents not one step closer to an understanding of the facts. Worse than that, they feel that instead of clarifying and stimulating thought, it puts it to sleep.

In so far as this has been true, orthogenesis deserves all the contempt with which it is held in some quarters. Certainly the paleontologists want to be very careful to purge themselves of every vestige of this sort of loose thinking before they take up the cudgels in its defence.

But on the other side, are the geneticists, having admitted the reality of orthogenesis, justified in dismissing it from further consideration because we do not understand its causes? If this is a proper attitude we should also drop all consideration of evolution itself for assuredly we know very little about its causes either.

If we agree that we have no comprehension of the causal factors at work there yet remains the very large task of mapping the evolutionary trends which are observed. And since some disbelieve in the very existence of orthogenetic trends, it may be advisable to reassemble the evidence which appears so convincing to the adherents of the theory. Yet it would seem that the old masters like Cope have done that well enough and that it would be better to refer to the literature. In any case, I shall not undertake this task but will concern myself merely with another side of the question. True or not, is the study of orthogenesis worth while?

It is an axiom that the value of a scientific theory depends not so much on its truth as upon its usefulness. The reason lies of course partly in the difficulty of ascertaining absolute truth and partly in that our problem is to master our environment. The question really

before us is then, I believe, not is orthogenesis true but is it of any good to us? Can we make orthogenesis bring forth useful results?

It is to that question then that after this preliminary clearing of the ground I would address myself.

Very definitely I believe that due consideration of the conclusions which orthogenesis demands would greatly strengthen taxonomy if indeed it did not give us a whole new outlook upon the plant and animal kingdoms. For I believe it can be demonstrated not only that evolution proceeded orthogenetically but that the orthogenetic lines in many groups of organisms, both animals and plants, have pursued similar trends, in other words that evolution runs a definite course and that the course has followed the same paths in entirely unrelated phyla.

For that reason I have entitled my discussion *The course of evolution.*

I. AGGREGATION AND MULTIPLICATION

The first stage in evolution, after the living units themselves have been produced, is aggregation or multiplication. This occurs at many levels all along the line from the lowest to the highest. (1) Dividing cells, failing to separate, form colonies and multicellular animals. (2) In the fern-allies, the sporophylls become aggregated into cones which are the starting point for all the complex evolution of the flower. (3) In the lower invertebrates, segmentation into a series of similar somites, as in the annelid, lays the foundation for most of the evolution of the animal body.

(4) In corals and jellyfishes, where asexual reproduction by budding plays a large role, the daughters often fail to separate and make possible complex polyzoid individuals closely resembling the colonial vorticellas except that the bells are multicellular individuals instead of single cells.

(5) The single meristems of lower ferns and cycads multiply in higher types until a freely branching plant body is produced. Exactly similar branching bodies with many terminal branches are produced in a number of unrelated groups of sedentary animals such as ascidians, sponges, bryozoans, and in at least one crustacean, *Thompsonia.*

(6) In the highest flowering plants the flowers, originally solitary, become aggregated into clusters with reduction of the subtending leaves to bracts and the clusters take on an individuality of their own, and become the well-known composite heads of the aster family.

Here special leaves simulate sepals, special flowers, petals, etc. This achieved, the composite clusters start out on an independent evolution of their own, repeating many of the steps earlier taken in the evolution of the solitary flower.

(7) Again in the grass family, we find the individual flowers, reduced to their lowest terms, associated first in loose panicles, then brought close together until, in all but the very lowest bamboos, the aggregate becomes a new unit, the spikelet, which again goes through a complete cycle of evolution on its own level. (8) Then clusters of spikelets go through another parallel cycle of evolution on a higher level, until finally such a complex unit as the ear of maize appears on a still higher level.

In short, wherever you find organisms or organs tied together in permanent association, you may expect to find the development of a new unity and the beginning of a new cycle of evolution.

(9) Even where the units are not stationary, something of the same nature occurs as, for example, in the social insects where assuredly the organic unit is the colony like the hive of bees and not an individual such as the worker. The queen bee has become essentially only an organ of the colony—its ovary. True, she retains her eyes, legs, wings, and other organs but so, in the multicellular body, does every cell retain the fundamental structures and functions of the original free-living protozoon.

I need hardly add in these troublous times that most of the problems of human society spring from the fact that we have not yet learned how to associate in larger units and that, if we do not exterminate ourselves in the process, evolution will surely carry us into some form of collective unity. Already this industrial age has made impossible any such individual independence as that of our pioneer grandfathers who settled this continent in isolated self-sufficient groups.

In studying the evolution of any one of these aggregates, we see that in some way living units in close proximity inevitably influence each other's development, and here we approach an understanding of the cause of orthogenesis. We may return to seek explanatinos later, but now we must go on with the process itself.

As has appeared from the mere catalog of various types of aggregates, aggregation is the foundation on which later evolutionary processes are built. Once the aggregate—colony, tree, flower cluster, or society—has been established, evolution follows a rather definite course.

II. REDUCTION

A. *Reduction in number of similar parts*

The next stage after the preliminary aggregation has been completed is a reduction in the number of similar parts.

Flower parts.—The lowest flowers, both monocot and dicot, like magnolias, buttercups, sagittarias, anonas, potentillas, and waterlilies, have large numbers of flower parts: 50–100 sepals, petals, stamens, and/or carpels as the case may be. That these are really the most primitive of the flowering plants is evidenced by the fact that in these types, and in no others, monocots and dicots come close together. The flowers of the dicot buttercup and the monocot *sagittaria* are practically indistinguishable. All of the higher types have the parts reduced to smaller numbers: 6-5-4-3. In many cases there are vestiges of the larger numbers formerly present.

There is, further, good evidence that various types of both dicots and monocots have radiated from a common type similar to the polymerous buttercups and *Sagittarias*.

Gill arches.—A similar reduction in the number of gill arches occurs in the lowest chordates. *Amphioxus* has 100 or more. In the cyclostomes, *Bdellostoma* has 15 to 10, other cyclostomes 9 or 8. In the elasmobranch sharks, *Heptanchus* has 9, *Chamaeselachus* 8, but the usual number is 7; while in ordinary fishes it is reduced from 6 in the embryo to 4 in the adult, but some fishes have lost one or two of these, leaving 3 or 2.

Segments.—In a general way, the phylogenetic order of several classes of invertebrates corresponds with the number of their somites. Annelids have more segments than millepedes and, of course, are far more primitive. Millepedes have more than centipedes; centipedes more than scorpions; scorpions more than insects.

Among crustaceans, branchiopods like *Apus*, with forty to sixty-three pairs of trunk limbs, are nearer the aboriginal type than *Malacostraca* like the crayfish with fourteen trunk appendages, and they in turn are more primitive than hermit crabs and true crabs which have lost or nearly lost their abdominal appendages.

Vertebrae.—The lamprey may have 400 vertebrae. Among the elasmobranchs, *Alopias* may have more than 200 in the tail alone, *Raja* about 150, while *Heptanchus* has only a few more than 100. The cod has 52, man 33.

Teeth.—The sharks have several hundred teeth. Teeth are still very numerous in the teleosts and may be present on all the bones of

the mouth. In the Amphibia, there is in general a considerable diminution in the number of teeth as compared with the fishes, but they still occur regularly on vomer and palatine in addition to maxilla and premaxilla and sometimes develop on the parasphenoid as well.

In reptiles the teeth are still numerous and widely distributed on several oral bones.

Up to the mammals, there is generally an indefinite succession of teeth throughout life, so that any loss is promptly replaced. The European viper, for instance, has as many as nine poison fangs in reserve which come into play successively as their predecessors may be torn out.

In the mammals, succession is reduced to the familiar two sets of teeth, and there is a plain tendency both further to reduce the number and do away with the division into two sets. The opossum has fifty teeth, but the ideal placental would have only forty-eight, and on account of losses here or there none exceeds forty-four except some of the whales whose teeth constitute a special problem. To be more specific, the dental formula of the dog is $\frac{3\text{-}1\text{-}4\text{-}2}{3\text{-}1\text{-}4\text{-}3}=42$, but in the cat the teeth are reduced to $\frac{3\text{-}1\text{-}3\text{-}1}{3\text{-}1\text{-}2\text{-}1}=30$. The lynx is made a separate genus because it has lost the first premolar of the upper jaw, and brought the dentition down to $\frac{3\text{-}1\text{-}2\text{-}1}{3\text{-}1\text{-}2\text{-}1}=28$.

The losses of specific teeth among the mammals, however, are obviously of a different character from the general reduction in number met in the lower classes and bring us to the consideration of the next type of orthogenetic trend.

Before going on, however, a caution should be noted.

Nobody should suppose that in any of these cases, we are attempting to cite actual lines of descent. The evidence indicates, rather, and I think most students would agree, that the actual ancestors of the higher forms listed passed through stages where the organs in question (not necessarily the whole organisms) corresponded with the earlier stages given.

Nor could it be maintained that recognition of the sequence in such cases as have been given could be of much use to taxonomy. In most of these cases everybody recognizes the more primitive types

from other criteria. Useful applications of this and the other principles to be given are to be had in working out the status of smaller groups which are made up of species much more closely related. For illustrations of this sort, I must turn back to the plants which I know better.

Take the tribe of grasses known as Festuceae. In *Eragrostis major*, there are 40 to 10 similar flowers; in *Eragrostis minor*, 20 to 8; in the related blue grass, *Poa pratensis*, 5 to 3. In *Cynosurus*, the fertile spikelets are 3- to 2-flowered. *Lamarckia* has numerous vestigial flowers in the sterile spikelet, and in the fertile, one perfect flower with vestiges of a second.

In the Chlorideae, *Leptochloa* has 12 to 3 flowers; Eleusine 7 to 3; *Gymnopogon* rarely 3 or 2 but normally only 1; *Bouteloa* several flowers, all but one vestigial; and *Cynodon* is constantly one-flowered.

In the Hordeae, *Agropyron Smithii* has 13 to 7 flowers; *Agropyron repens* about 5, *Agropyron pauciflorum* 2, barley and all the highest most specialized genera are reduced to one flower.

In the higher tribes of grasses, the spikelets are uniformly one-flowered, but vestiges of a second flower are usually present. These are, however, in different relations to the fertile flower, thus indicating independent but parallel reduction from different ancestors.

B. *Fixation in the number of parts*

The third of the orthogenetic trends I shall mention is inextricably associated with the preceding. Not only are the numbers of parts reduced but the number is fixed. In the earliest stages, the numbers are large and indefinite. They become smaller and definite.

Not only do mammals have less teeth than the lower groups, but the number of teeth is nearly always constant, and even varies comparatively little even in the large groups. Not only are the petals of ordinary flowers reduced to 6-5-4 or 3; they are, with only minor aberrations, fixed at 6 or 5 or 4 or 3, and as all of you know, these numbers are characteristic of whole families or even orders.

The same trend occurs in the higher level of the flower cluster of the aster family. In most composites, the number of disc flowers, ray flowers, and bracts is large and indefinite; but here and there the head has been reduced to a definite organization. Thus, in Cosmos and related genera, there are 16 bracts in the involucre in two sets of 8 each and 8 ray flowers, each set alternating in position with the one outside it. In our common *Chrysogonum*, the involucre is made up of 10 bracts in two sets of 5 each, the inner of which wrap around the

ovaries of the 5 fertile flowers. Other flowers are present but vestigial.

So on down the list in each of the illustrations cited above and throughout nature generally, the numbers of parts become fixed and standardized at a relatively early stage in evolution; and thereafter the reductions which occur are, like the loss of the vestigial premolars in the lynx, very minor compared with the wholesale reduction that occurs earlier.

C. *Consolidation*

At a third stage in the reduction process, other tendencies begin to creep in which later become manifest in the development of new units. Primitive types are loosely knit. During the course of evolution they become more and more compact.

In plants, consolidation expresses itself especially in the organization of flowers and flower clusters. Primitive flowers were solitary. Next they began to aggregate into loose clusters, the stems of these shortened produce simple *racemes;* further shortening of branches gives rise to unbranched *spikes;* the main axis then shortened, drawing all the flowers down into a compact *head.*

Similarly the axis of the individual flower is shortened from the primitive condition of a pine cone seen in *Magnolia* to the stage of most flowers where the parts, instead of spiralling up an elongated axis as in the cone, are in circles one above another.

Although this completely-eliminated axis might seem to represent the theoretical limit, stoppage of axial elongation goes much further in many families where the axial growth is inhibited before lateral growth is complete, with the result that the lower parts pile up around the center and the flower turns itself inside out, so to speak. Thus, an epigynous flower is produced in which the parts originally basal—sepals, petals, and stamens—are carried up around the ovary. In some cases, as in four-o'clocks, roses, and lythrums, the tube grown up around the ovary remains free from it but in a large majority of such flowers, the elevated parts grow fast to the ovary as in apples, melons, blueberries, and gooseberries.

This orthogenetic trend is so characteristic and prevalent that it appears independently in many unrelated orders. To those mentioned we might add honeysuckles, composites, lobelias, cacti, begonias, aralias, carrots, and hydrangeas.

The mouth parts of arthropods, originally the segmental appendages of the somites in the oral region are in all but the lowest forms brought into close contact and fitted together around the mouth. As

in the flower clusters there is remarkably little tendency toward fusion of the separate appendages.

Our own skull is as notable an example of this sort of thing as any. The skull of primitive vertebrates consisted of a loose basket-like aggregation of separate bones in which the mandibular, the auditory, the ocular, and even the olfactory regions were distinct units hung around the cranium but by no means a part of it. Here again although complete unity has been achieved by closely interlocking sutures, there is remarkably little fusion of bones.

The same tendency toward consolidation of loosely arranged structures is manifest in the nervous system of arthropods. The primitive groups have a double chain of ganglia strung along the length of the body. But the commissures between these have shortened up in all higher forms. Here, as in the development of inferior ovaries in flowers, the consolidation of the parts carries us much further, into another type of reduction which is the next step.

D. *Coalescence of free parts*

The fusion of parts originally separate is carried out even more conspicuously in flowers by horizontal fusions than by the vertical concrescence around the ovary described in the development of flowers with inferior ovaries.

The recognized distinction between lower and higher dicots is in the fusion of the separate petals, such as we find in pansies, into united corollas, as in petunias. Traces of the originally separate petals remain as ribs of the united corolla as in morning-glories or as projecting lobes as in phloxes. While all of the highest dicots thus have sympetalous corollas, there is abundant evidence that fusion really occurred and/or perhaps is still occurring over and over again independently in scores of families, as for instance in the Leguminosae where the flowers are certainly polypetalous but show varying degrees of fusion in many different genera. In the heath family, Labrador tea has separate petals but in most of the genera they are fused as in Azalia and Mountain laurel. In the olive family, the petals of fringe-tree and forsythia have barely united at the base, but those of lilac are joined half-way up.

All the other flower parts show the same tendency, and there is every evidence that fusion has occurred independently in many unrelated families. Thus we have united sepals in the calyx of a carnation, united carpels in innumerable fruits like orange, apple, banana. melons, etc. etc.

The trend toward fusion frequently reappears in clusters of flowers. Thus, a mulberry (*Morus*) resembles a blackberry, but while the blackberry is produced by the partial coalescence of the carpels of one flower, the mulberry is due to the fusion of many flowers, each one of which becomes a lobe of the fruit; and this tendency, manifested in various ways, is characteristic of the whole family Moraceae, e.g., bread-fruit and fig.

A pineapple is a similar aggregate. The fruit which we eat includes the bracts as well as the ovaries of the many flowers as can be readily demonstrated by inspection of the fruit or more clearly yet, of the numerous showy blossoms at flowering time.

Fusion of parts originally free is equally marked in animal organs. Everyone who eats chicken notes that the backbone in which the vertebrae, which may still be readily counted, is united into two units, one supporting the wings and the other the legs. That this consolidation has developed in the class Aves is shown by a glance at *Archaeopteryx* where there is little more fusion of vertebrae than in reptiles.

The segments of the originally simple arthropod body have been consolidated, as everybody knows, into the most highly differentiated cephalothoracic regions of insects, crustaceans, and spiders until decision as to the exact number of segments of the aboriginal ancestor has become as difficult as in the vertebrate skull.

The brain of arthropods and apparently that of vertebrates also originated in similar fashion.

E. *Elimination of some organs*

After large and indefinite series of organs have been reduced to small and definite numbers, the next step in the reduction process is the complete elimination of some sets.

Among flowers, the loss of petals or sepals or stamens or carpels is exceedingly common. Very often elimination has not been quite complete and tell-tale vestiges of the lost organs remain.

Elimination of floral organs has occurred, so to speak, both wholesale and retail. There are whole regions of the Angiosperms where the flowers have been reduced almost to their lowest terms such as the grasses, sedges, willows, hickories, oaks, birches, and spurges. Many individual genera or even single species in families with complete flowers have also suffered similar losses, as for example *Isnardia* in Onagraceae, *Aruncus* in Rosaceae, some species of ash in Oleaceae.

Great confusion has resulted among botanists from failure to

understand that these flowers are reductions. It used to be supposed that such rudimentary flowers as willows and poplars were primitive and that evolution had proceeded by the addition and division of parts until finally the complete polymerous flowers of buttercups were achieved. There is no occasion here to go into the merits of this old controversy. Suffice it to say that if the terminal reduced twigs of the phylogenetic tree are regarded as relics of former main trunks, it is as difficult to find the connections with the roots as it would be if a similar attempt were made with an oak tree. Worse yet, each separate twig would require a different root and the family tree would become polyphyletic with a vengeance!

One of the most fundamental eliminations of organs is in the sex organs of the vertebrate. The male and female sexes start development alike, clearly pointing back to a primitive hermaphroditic condition. The embryo lays down two urinogenital outlets on each side, the Wolffian and the Muellerian ducts. In the male, the Wolffian duct becomes the seminal duct and the Muellerian atrophies. In the female, the Muellerian duct becomes the Fallopian tube and the Wolffian atrophies.

Eliminations in animals are so numerous and generally recognized that there is hardly need to point them out. Snakes have lost all their limbs, and some boas retain vestiges to prove it. Whales and sea cows have lost their hind limbs. *Dinornis* has only the slightest vestiges to show that it ever had wings, and other flightless birds like cassowaries, apteryx, and the ostriches show various stages in the loss of their wings.

III. DIFFERENTIATION

A. *Differentiation of parts originally similar*

Soon after the number of parts is fixed, differentiation sets in. Parts originally similar become specialized to subserve diverse functions. Similar spike teeth segregate into incisors, canines, and molars. The vertebrae, all alike in the fishes, diversify until each one takes on peculiarities of its own.

In flowers, the regular radiate blossom with petals all alike becomes a very irregular lipped flower like an orchid, a pea, or a snapdragon. All stages of the process may be seen in many unrelated families. The lowest member of the figwort family is the familiar mullein with almost regular flowers still retaining the primitive 5 stamens. From this there is a complete series to the most irregular flowers like snapdragons and louseworts in which the stamens are reduced to 4 or 2

and twisted out of all semblance to the straight and regular organs of the ancestral flower.

In the Leguminosae, all transitions from regular flowers like *Mimosa* through *Cassia* down to the highly one-sided peas are familiar.

No such series occurs in the orchids, all members of the family having very highly one-sided flowers, but botanists place orchids at the summit of the monocots for exactly this reason. That is, though the stages in their differentiation are gone, we recognize the applicability of the rule in assigning them this position.

B. *Progressive sterilization*

The original and most fundamental differentiation was the sterilization of most of the cells in the body. In the original unicellular organisms all cells were of course reproductive. The most primitive colonies are in the same condition. But very early reproductive functions were restricted to special cells. From that time on, a large part of the course of evolution has centered around a continuously progressive sterilization of reproductive tissues with accompanying differentiation of the sterilized elements into vegetative organs.

This is hardly the place to call attention to the fact that the so-called "race suicide" of the cultured classes, which bothers us so much, is a homologous biological phenomenon. How serious it may become we cannot guess, but we may remark that there was probably no occasion to worry over the "suicide" of the first brain cells.

But this aspect of progressive sterilization, followed by differentiation, brings us to another well-known characteristic of living organisms.

IV. SUBSTITUTION OF ONE FUNCTION FOR ANOTHER

All of you are familiar with the fact that almost every new organ of animals and plants consists of an old one made over to serve a new function.

Stamens and carpels are clearly "made-over" leaves. This is not manifest from inspection but is clearly demonstrable by study of comparative anatomy.

Similarly, petals and sepals are as definitely sterilized stamens made over into new functions. While the original differentiation of sepals and petals occurred in the unknown ancestry of the Angiosperms, the orthogenetic tendency in that direction continues in many families.

The flower of canna has its full complement of both sepals and

petals, but those are not what you see when you look at a canna flower. The conspicuous part of this flower consists of sterilized stamens enlarged and made petaloid. Only one-half of one stamen remains functional, riding like an appendage apparently out of place on the big staminode to which the rest of it has been transformed.

The tendency to make stamens over into petaloid structures is pronounced throughout the higher monocot families, viz., in bananas, gingers, arrowroots, and orchids as well as in cannas.

But the same tendency is latent in many families of flowering plants, dicots as well as monocots, even though it does not normally come to expression. Many of the "double" varieties, which occur in almost all types of ornamental plants, are produced simply by the conversion of stamens into petals, as you may see by comparing wild roses with our hybrid tea types.

The metamorphoses of fins of fish to legs, of the forelegs to flippers in whale, to wings in bats and birds, are too familiar to be mentioned. The scales on the top of the fish's head became part of the bony skull.

It is so obvious that there is no need of saying it that a species with metamorphosed structure has been derived from one unchanged. The point for us here is that such metamorphoses take a long time, that there are many stages in the process which therefore constitutes an orthogenetic trend.

V. ANNEXATION OF ACCESSORY PARTS

The tendency toward consolidation often goes far beyond the organs immediately concerned. It seems as though a definite principle of organization grips all living structures which come close enough together to establish interrelations.

Many familiar examples will occur to you. The scales of the winter bud which protect the head of dogwood flowers expand at flowering time into the large white petaloid structures which make the dogwood so beautiful. The topmost leaves of the poinsettia take on the bright red which makes them desirable for Christmas decorations. The leaves below the head in the composites are brought into the organization and become analogous to sepals. The bracts subtending the flowers of grasses, becoming glumes, carry on the subsequent evolution of the group. In some grasses, where the spikelets are brought down close to bracts of a second order, these in turn are taken into the organization and become functionally comparable to glumes, as in the husk of maize or the hull of a sand burr.

Again when in composites the heads with their bracts are brought

close together in the axils of lower leaves, these may become to all intents and purposes involucral bracts, and the compound head starts on a new line of evolution as in our common *Elephantopus* where the marginal ray flowers radiate, not from each head, but from the center of the cluster of heads, making the cluster analogous to a single flower.

In the pineapple, pulpefaction spreads from the ovaries through the bracts, and in some tropical varieties when fully ripened, to the main axis of the flower cluster as well.

The fact that our unified vertebrate head was achieved by the addition of gill arches and other organs originally separate entities has already been alluded to.

VI. THE NARROWING POSSIBILITIES OF EVOLUTION

As the evolution in any group proceeds the possibilities of diversification continually contract.

In the beginning, unrestrained by heredity, variations had free rein. The differences among unicellular organisms are more fundamental than those between the most diverse of the higher organisms. Blue-green algae, diatoms, ciliates, rhizopods, slime molds, and bacteria differ far more among themselves than do higher plants from higher animals. Among the bacteria, for instance, we have one group which has built its metabolism around the oxidation of sulfur, and another which oxidizes iron as a source of energy, while the protoplasm of all higher organisms is built on carbon chemistry.

The cytology, nuclear behavior, and consequently the heredity of all higher organisms, both plants and animals, is essentially the same. Otherwise, Mendel's law could not hold in guinea-pigs as in peas. But among unicellulars there are several entirely different types of cell organization the mechanism of which would preclude Mendelian inheritance.

Like most other laws of evolution, this narrowing path of progress finds a perfect analogy in human artifacts. Take the automobile. Those of you who can remember the early days of "horseless carriages" will recall the fundamental diversity of the early types. Beside gas buggies, there were steam and electric carriages. They were high-wheeled and low-wheeled with cushion tires, as well as pneumatic. Among the gas engines, some had one cylinder, some two, as well as others with four. A fundamentally different type of transmission survived for many years in the old Model-T Ford.

The history of the automobile gives a clear answer to the cause of

the phenomenon. The diverse early types were eliminated by what amounts to natural selection. As the better types were proven out in use, it became impossible to sell the others until today all cars have approached so closely to a common standard of excellence that there is little to choose among them and the manufacturers fearing to adopt radical departures such as putting the motor in the rear have begun to waste their energies on inconsequential gadgets.

This is exactly the situation among organisms. In the early stages, protoplasm can go off into all sorts of experiments but as the type becomes fixed, heredity restricts variations to minor features and in the end we get mere diversity without any real difference. Many authors have called these later stages "speciation" and have emphasized the differences between speciation, evolution with a small *e* and Evolution of the larger characters, Evolution with a big E.

Dollo's well-known "law of the irreversibility of Evolution" is, of course, only a special case of the broader law of the narrowing possibility of variation.

Only two examples of the fundamental diversification which occurs in primitive groups may be given. Among primitive Notoungulata, a fossil order of hoofed mammals peculiar to South America, Simpson[4] found in the animals in a single quarry, i.e., those living together as one species in one time and at one place, characters upon which had been based seventeen species, seven genera, and three families.

The important consideration for us is: the criteria by which these families, genera, and species had been founded constitute valid distinctions for separating such groups among the later, more advanced members of this same order.

Among plants, the primitive family Anonaceae has more different kinds of floral structures than are to be found in any other one family, some of them not duplicated anywhere else among flowering plants. Yet indubitably all are closely related and properly placed in a single family.

This narrowing of the path of evolution seems to me to refute the claim of the geneticists that mutations are purely at random. You might as well argue about the random aberrations of a canal boat swinging on its tow-rope as compared with the course of a ship on the open sea, as to conclude that the random mutations of *Drosophila* tell us much about the evolution of insects.

I am not trying to minimize the importance of the mutations of *Drosophila*. They have been the key to wonderful advances in our

[4] SIMPSON, G. G. *Supra-specific variation.* Am. Nat. 71: 247. 1937.

understanding of inheritance. But their relation to the evolution of insects has yet to be made known.

Those inclined to believe that changes significant for evolution occur at random would do well to ponder the implications of a paper by one of the greatest of geneticists, N. I. Vavilof, entitled, *Homologous variation.*[5] Assembling all the species and varieties of cultivated plants and their relatives in his experimental gardens, Vavilof observed that related types repeat over and over again the same series of characters, i.e., that homologous mutations had occurred in related types.

For instance, there are three groups of wheats. In the first group, *Triticum compactum* and *T. spelta* are closely allied to *T. vulgare* and repeat all the varieties of it.

The second group repeats the varieties of the first, e.g., there are varieties with white, red, and black ears; smooth and hairy ears; with white and red grains; winter and spring wheats; only beardless varieties are unknown.

The third group repeats the varieties of the second.

The similarity of the characters of the varieties of the three species of pumpkins, *Cucurbita maxima, C. pepo* and *C. moschata* interested Darwin who thought it accidental. Vavilof brings it under the reign of his law of Homologous variation. He shows further that the species of related genera show the same homology in their variation. Thus *Cucurbita* (pumpkin), *Cucumis* (cucumber), and *Citrullus* (watermelon), all have types with fruits round, oblong, flat and segmented; white, green, yellow, brown, black; monochrome, streaked, or spotted; each has both sweet and bitter varieties; and all show homologous variations in color and hairiness of petals.

He lists 34 homologous variations that have occurred in both wheat (*Triticum*) and Rye (*Secale*) and shows that the related genera *Agropyrum* and *Aegilops* though studied in less detail repeat in general the same series.

Following up his belief in homologous variation Vavilof sent out expeditions to search for varieties with characters known only in related types and was successful in finding them, very much as the chemists have filled the gaps in the periodic table of the elements.

The very homology in the mutations responsible for these characters by itself disposes of any supposition that they occurred at random. The same force must have acted independently in each of these parallel mutations.

[5] Journ. Genetics 12: 47–89. 1922.

While much of the convergence observed in plants and animals is clearly adaptive like the streamlined bodies of fishes, whales, seals, and manatees, most of the homologous characters dealt with by Vavilof are of no conceivable use to the organism and furnish no handle for natural selection to take hold of.

If they were useful their adaptiveness would necessarily be alternative. That is, natural selection would have preserved the more useful, for example, say leaves without ligules, and eliminated the others, leaves with ligules.

APPLICATION OF ORTHOGENESIS TO RESEARCH

I have listed some of the orthogenetic trends characteristic of organisms, and I have given data enough, I think, to prove their reality. Certainly more could be supplied to the extent that time and space permitted. Our further task is to apply such information to the problems of taxonomy.

One illustration of the use of those considerations, which occurred right here in our midst, was Hitchcock's treatment of the grasses. When he wrote the Gramineae for Gray's *Manual* in 1908, he used the old conventional system which put maize at the beginning, but in his *Genera of grasses* 1920, he adopted a system in accord with the orthogenetic trends here listed.

The difference in the mind of a student is very much the same as the enlightenment which suddenly dawned on all biologists when they first looked at organisms from the point of view of evolution. Like the theory of evolution itself it gave meaning and coherence to a mass of heterogeneous detail which before had been merely a burden on the memory.

If it be granted that every group of plants should be set into such an orthogenetic order and that the same should be done for animals, it must be recognized that the accomplishment of such an undertaking is a task not only of large magnitude but of considerable difficulty as well.

It might seem that, given the guiding principles, any child could make the applications. But it is not so. Although these orthogenetic trends are general characteristics of organisms, they are not organismal.

Each trend pursues its own course independent of all the other trends to which the organism is subject. One genus may have gone far in reducing the numbers of its parts but have made no progress in differentiation or in the fusion of parts. Another genus in the same

family will show much differentiation but retain a primitive number of parts. That is, most close-knit groups of organisms can be arranged in various ways, depending on which of the orthogenetic trends present is used as the basis of classification. The problem of the taxonomist is to decide which of the trends present is most significant in the case in hand.

COMPETITION A POSSIBLE EXPLANATION OF ORTHOGENESIS

Before closing it will be well to take up the question of the cause of orthogenesis which I sidestepped at the beginning. I repeat that whether we understand it or not, orthogenesis must be accepted as the way of evolution. Yet we will never be satisfied until we penetrate the mystery and reveal the cause. It is unnecessary to say that I am not prepared to discuss this question with any degree of assurance or of specification, but there are some simple and well-known biological principles which may have a large bearing on the problem.

Why should there be a reduction in numbers of parts? Remembering that in the beginning of aggregation of cells—and to a considerable extent ever since—each individual cell maintains its own fundamental entity, we may ask why some should be eliminated. The answer comes to our lips almost automatically: It is the fittest, or more accurately, it is the most favorably placed, that survive.

In marvelling at coordination characteristic of multicellular plants and animals, we are apt to forget that their individual cells and organs are still in competition with each other. But we see examples of this fact every day in the buds of a tree which are laid down in numbers far beyond the possibilities of development. If some are removed, others which could never have developed in the presence of more favored competitors begin growth. It has been proven that the dormant buds are suppressed by the growth of the dominant ones. There is a metabolic gradient from the dominant leader backward and inhibiting hormones are sent back from the leader which prevent the growth of subordinate buds.

Similar metabolic gradients are characteristic of the animal body. They have been studied extensively by C. M. Child. He found that the orientation of the body is definitely controlled by these metabolic gradients. In simple planarians he was able experimentally to alter the metabolic gradients. By doing so, he was able to shift the head of the animal around almost at will.

No one has attempted to see how far metabolic gradients could be instrumental in directing the evolution of the race as they certainly

do determine the development of the individual. In view of the similarity of the two cases there is no more occasion for assigning mystical agencies as the cause of orthogenesis than there is for bringing them into the explanation of the development of the individual.

Again a geneticist would say that the variations reported by Vavilof are homologous because the genetic constitution of related types is homologous. Given the closely similar gene complexes, closely similar mutations would be expected. This again is, however, only a restatement of the Law of the narrowing possibility of evolution.

Finally, it should be pointed out that these orthogenetic trends are largely unadaptive. In a few cases,such as the differentiation of the teeth, advantages to the organism may be made out. But generally, nothing of the sort can be imagined. For the most part, the adaptive sequences in evolution are superposed on the great orthogenetic trends but are entirely independent of them.

In the spurge family, Euphorbiaceae, for example, there is an orthogenetic series in the reduction from fairly typical flowers down to vestiges which could never be recognized as flowers if we did not have a complete series of integrating transitional forms. But no one could pretend that this change is advantageous. Alongside this, and entirely unrelated to it, is a modification of the plant body from that with typical leafy shoots into a series of leafless desert plants so similar to the cacti that they can be told apart only by technical characters. The independence of orthogenesis from environmental stimuli has been pointed out by many writers and there is no time to elaborate or further to illustrate here.

Our concern with the lack of adaptiveness in the main trends of evolution is its relation to the claims of the geneticists. In their belief, the orderliness of nature has been brought about entirely by the elimination of unfit mutations through natural selection.

Thus their case is entirely dependent on a demonstration that all trends observed in the evolution of all groups are adaptive, i.e., so useful to the organism that natural selection can take hold of them. It appears to me, as it has to others, that it is fairly easy to show that many of these trends are not so related.

I have alluded to a few instances of this but there is no time tonight to take up the evidence in detail.

So here I must rest my case.

PROCEEDINGS OF THE ACADEMY AND AFFILIATED SOCIETIES

CHEMICAL SOCIETY

502ND MEETING

The 502nd meeting was held in Corcoran Hall, George Washington University, on Thursday, October 13, 1938, with President DRAKE in the chair. After the reading of the minutes, the President thanked the authorities of the University for the use of the meeting rooms. He next outlined to the membership the newly adopted plan of informal meetings to be sponsored by the Society. These meetings are to be held at irregular intervals, the object being the promotion of a fuller discussion of topics of considerable interest, particularly in connection with recent advances in chemistry, and to further the interests of special groups of chemists within the Society. The presentation of the subject matter at these meetings is to be informal, with an ample opportunity for a full and free discussion.

The following program was presented in three sections:

Analytical and Inorganic Chemistry, G. E. F. LUNDELL presiding:

BOURDON F. SCRIBNER: *The operation of a spectrographic laboratory.*—Both prism and grating spectrographs applicable to analytical work are commercially available. The prism types are of the Cornu or Littrow designs and the grating spectrographs of the Abney and Eagle mountings. The equipment for a laboratory should consist of a spectrograph costing $1,000 to $3,000 and accessory apparatus for excitation of spectra and examination of plates, costing from $300 to $1,000. In addition, a dark room for photographic processing and chemical facilities for preparation of samples are required.

The laboratory at the National Bureau of Standards is equipped with a large stigmatic grating spectrograph with a dispersion of 5 Ångstrom units per mm. and a large quartz Littrow spectrograph with accessories. The analyses made are (1) qualitative examination of samples for 55 to 70 elements, using a micrometer comparator; (2) rough quantitative analysis to ± 10 per cent of the amount present, by direct comparison of the spectra of the unknown and a series of standards; and (3) refined quantitative analysis to ± 3 per cent of the amount present using a densitometer and plate calibration.

The qualitative analysis, in which the concentrations of the elements present are estimated to a factor of 10, is applied to tests of purity, surveys preliminary to chemical analysis, identification of precipitates and concentrates, and comparison of museum specimens. Quantitative analyses in the range of concentrations below 10 per cent are made of tin and iron and of various constituents in steel, zinc, gold, refractories and water residues. (*Author's Abstract.*)

C. J. RODDEN: *Some observations on the chemistry of the rare earths.*—The abundance and sources of the rare earths with the general methods of separation were described with comments on the newer methods of isolating the rare earth elements. The physical and chemical properties were described showing the characteristic absorption spectra which were taken using but 0.3 to 0.5 ml. of solution. The use of the physical properties was indicated in the separation of the elements. The analytical chemistry up to the present was commented on with emphasis on the lack of methods for determining the separate elements. A survey of the general uses of these elements and their

salts showed that the uses up to the present are meager. (*Author's Abstract.*)

W. D. URRY: *Isolation and measurement of small quantities of helium from radioactive decay.*—No abstract received.

Organic chemistry, S. N. WRENN presiding:

R. P. JACOBSON: *Structure of Sarsa-Sapogenin.*—From a study of a number of transformation products of sarsa-sapogenoic acid it is concluded that this substance contains in the side chain a γ-keto acid grouping attached to a substituted tetrahydrofurane ring. The side chain characteristic of the steroid sapogenins probably contains two tetrahydrofurane rings corresponding to the formulation first proposed by Tschesche and Hagedorn. (*Author's Abstract.*)

J. R. SPIES: *Chemical study of some constituents of the croton bean* (C. tiglium *L.*).—The author's work on the fish-poisoning and vesicant principle of the croton bean (*C. tiglium* L.) was reviewed. The aglycone fragment of the croton bean nucleoside (2-oxy-6-amino-purine-d-riboside) could not be deaminated with nitrous acid. The isogaunine from this nucleoside was deaminated, however, by refluxing with constant boiling hydrochloric acid. The xanthine so obtained was identified by analysis and by its transformation into bromocaffeine and ethoxycaffeine. Isoguanine crystallizes in rosettes as a hydrate containing one and one-half molecules of water of crystallization ($C_5H_5ON_5 \cdot 1\frac{1}{2}H_2O$). Isoguanine was cited as an unusual compound which apparently cannot be deaminated with nitrous acid but can be deaminated by refluxing with constant boiling hydrochloric acid. 2-oxy-6-8-diamino-purine was obtained from isoguanine by coupling it with 2-4-dichlorodiazonium chloride and reducing the red coupling compound. The sulfate, hydrochloride, acetate, carbonate, and picrate of 2-oxy-6-8-diamino-purine have been prepared and the formulas of these salts were determined. All of these salts are crystalline and exhibit birefringence when viewed with a polarizing microscope. Unlike isoguanine, 2-oxy-6-8-diamino-purine forms stable salts with both acetic acid and carbon dioxide. (*Author's Abstract.*)

HORACE S. ISBELL: *The nomenclature of the sugars and their derivatives.*—The various proposals which have been made for renaming the sugars show the need for the adoption of a definite policy for naming the higher sugars and their derivatives. E. Votocek (Collection Czechoslov. Chem. Communications **10**: 264, 1938) has suggested substituting *d* or *l* for Fisher's α and β or Elsner's *a* or *b* (Tollens-Elsner *Handbuch der Kohlenhydrate*, 4th Edition, page 391). Thus *d*-α-glucoheptose or *d*-gluco-α-heptose becomes *d*-gluco-*d*-heptose. In the latter name the first *d* refers to the configuration of the terminal asymmetric carbon, while the other *d* symbol refers to carbon 2. Hudson (J. Am. Chem. Soc. **60**, 1537, 1938) has suggested calling the same product *D*-gluco-*D*-gulo-heptose. In this name the first *d* or *l* symbol refers to the configuration of the terminal asymmetric carbon, while the second refers to the configuration of the fifth carbon. Obviously if both proposals are used for naming new sugars, much confusion will result. The suggestion made by C. D. Hurd (Symposium on the nomenclature of the sugars, American Chemical Society, Milwaukee, Wis., September 8, 1938) to drop the first term in Hudson's proposed name and to substitute a series of letters to represent the configurations of the higher carbons would offer a good compromise provided the customary *d* and *l* nomenclature was maintained by using as the first letter a *d* or *l* symbol. For example, *d*-α-glucoheptose could be called *d*-*d*-guloheptose. In this name the first symbol represents the configuration of carbon 6, while the term *d*-gulo represents the configuration of carbons 2, 3, 4, and 5. If the names for the higher sugars are

to be based on the structurally related hexoses, the analogy should include the glycosidic carbon so that the alpha modifications of the heptoses will correspond to the alpha modifications of the structurally related hexoses. A classification of this character results by calling substances having like configurations for the glycosidic and ring-forming carbons alpha, and calling substances having unlike configurations from the glycosidic and ring-forming carbons beta. (*Author's Abstract.*)

Physical Chemistry, B. D. VAN EVERA presiding:

JACINTO STEINHARDT: *Solubility anomalies in crystalline proteins.*—The speaker reported on work performed in the Department of Physical Chemistry, Harvard Medical School, to be published in the Proceedings of the Symposium on Proteins held at Cold Spring Harbor in July 1938 in part, and also in the Journal of Biological Chemistry. No abstract was received.

GEORGE W. MOREY and JOHN S. BURLEW: *A filter autolcave for solubility measurements at elevated temperatures and atmospheric pressure.*—A new type of autoclave has been designed for the purpose of making precise solubility measurements in alkaline solutions at elevated temperatures and atmospheric pressure. With it a mixture of solid and liquid at a constant temperature can be stirred in a silver vessel and then filtered through a platinum felt, after which the filtrate is cooled and analyzed. The technique of such measurements is illustrated by data concerning part of the system $NaOH-Na_2CO_3-H_2O$ between 60 and 70° C. (A detailed description of this research appears in Am. J. Sci., **35A:** 285 (1938).) (*Authors' Abstract.*)

J. LESLIE JONES: *Kinetics of the thermal isomerization of cis-dichloroethylene.*—The kinetics of the gaseous thermal isomerization of *cis*-dichloroethylene into the *trans* form has been investigated over the temperature range 560–620° K. The change in the percentage composition of the gas phase was followed by condensing the product after a period of time and measuring the condensation vapor pressure of 0° C. A large scale calibration curve was employed to determine the percentage isomerization. The isomerization was found to be practically homogeneous after properly treating the reaction vessel. The rates of the forward and reverse reactions were found to be given by the unimolecular rate constants

$$k = 2.5 \times 10^6 e^{-27,100/RT}$$

and

$$k_r = 2.7 \times 10^6 e^{-26,000/RT}$$

respectively.

The simple theory of Hinshelwood is inadequate to account for such small values of the temperature independent factor, which is smaller than the usual value by a factor of 10^5. A theory is proposed to account for this abnormally slow reaction. It involved the loosening of one bond in the double bond, a relative rotation through 180° by one of the carbon atoms accompanying an inversion of one carbon atom and closure of the double bond. (*Author's Abstract.*)

FRANK C. KRACEK, *Secretary*